TAXONOMIC REVISIONS OF SIX GENERA OF ENTIRE-EYED OWLFLIES

(ASCALAPHIDAE: HAPLOGLENIINAE),

AND

FIRST LARGE-SCALE PHYLOGENY OF THE OWLFLIES

A Dissertation

by

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ABSTRACT

The family Ascalaphidae, or owlflies, is a cosmopolitan and charismatic but poorly-understood and taxonomically ill-organized family of Neuroptera (lacewings). Prior to this work, it comprised approximately 450 valid described species placed in three subfamilies, 15 tribes, and 100 genera. In this dissertation, six genera of Haplogleniinae, or entire-eyed owlflies, are taxonomically revised based on cladistic analyses of morphological characters, and the first comprehensive phylogenetic analysis for the owlflies based on morphological and molecular characters is presented.

The taxonomic revisions are presented in three chapters, with their results as follows: (i) *Allocormodes* McLachan, a genus of cryptically-patterned species broadly distributed across tropical sub-Saharan Africa, is revised based on analysis of 35 morphological characters. Eleven species are recognized (five new), and one species name is synonymized. (ii) *Tmesibasis* McLachan, a genus distributed across sub-Saharan Africa and the southwestern Arabian Peninsula, is revised based on analysis of 39 morphological characters. Ten species (two new) are recognized as valid, and two species names are placed as synonyms. (iii) The entire-eyed owlflies of the Western Hemisphere are revised based on analysis of 79 morphological characters. Before this study, this group comprised 25 extant and two fossil species in six genera. Based on the cladistic analysis, a new classification is proposed, which places 37 extant species (13 new) in four genera: *Amoea* Lefèbvre, *Ascalobyas* Penny, *Haploglenius* Burmeister, and

Neascalobyas new genus. Within *Haploglenius*, five new species groups are proposed, three of which represent former genera (*Ascaloptynx* Banks, *Neohaploglenius* Penny, and *Verticillecerus* van der Weele). Five species previously recognized as junior synonyms are also re-erected, and seven names are placed in synonymy with other species. In addition, *Episperches molinai* Navás and the fossil species *Amoea electrodominicana* Engel and Grimaldi are removed from *Amoea* and are placed within *Ameropterus* Esben-Petersen and Haplogleniinae *incertae sedis*, respectively. *Ascaloptynx oligocenica* Nel is also removed from the novel *appendiculatus* species group (formerly *Ascaloptynx*) within *Haploglenius*, and is placed within Haplogleniinae *incertae sedis*. For each of the genera treated, all species determined here to be valid are figured, keys to their identification are given, and maps of their distributions are provided.

In the fourth major chapter, the first large-scale phylogeny of the owlflies is presented, based on analysis of combined morphological (25 characters) and molecular (16S, 18S, and COI genes) datasets. These datasets were analyzed under maximum likelihood, Bayesian, and parsimony analytical regimes for 76 exemplars of Myrmeleontiformia (Ascalaphidae, Myrmeleontidae, Nemopteridae, Nymphidae, Psychopsidae), including 57 of Ascalaphidae. At the superfamily level, the families were recovered in all analyses in the form Psychopsidae + (Nymphidae + (Nemopteridae + (Myrmeleontidae + Ascalaphidae). Ascalaphidae was recovered as monophyletic in the Bayesian and parsimony analyses, and paraphyletic with respect to Ululodini and Myrmeleontidae in

the maximum likelihood analysis. The subfamilies Haplogleniinae and Ascalaphinae were not recovered as monophyletic in any analysis. The Ululodini were monophyletic and well-supported in all analyses, as were the New World Haplogleniinae and the African/Malagasy Haplogleniinae. The remaining Ascalaphidae, collectively, were also consistently monophyletic, and include a genus traditionally placed in Haplogleniinae, *Protidricerus* van der Weele. None of the included tribes of non-ululodine Ascalaphinae were monophyletic in any analysis. *Protidricerus* was discovered to express a well-developed pleurostoma, a feature previously only encountered in divided-eye owlflies, and this feature may be important in future classifications. The feature traditionally used to differentiate the Haplogleniinae and Ascalaphinae, the entire or divided eye, can no longer be regarded as a reliable spot-diagnosis character to separate monophyletic groups within the family, and should be re-evaluated.

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CHAPTER I

INTRODUCTION

Ascalaphidae, or “owlflies”, are found worldwide, and are highly specialized aerial predators of other flying insects. They come in many shapes and sizes, but generally resemble small to medium-sized dragonflies in the form of the body and wings and in the inclination of the thorax and legs (they differ conspicuously in having long, clubbed antennae). Many species are only active at dusk and/or nocturnally. As larvae, they are sit-and-wait predators that capture passing arthropods in their sharp-tipped jaws and immobilize them with paralytic venom, all before carefully sucking out their internal fluids.

Currently (Tjeder 1992), the family Ascalaphidae comprises three subfamilies: the Albardiinae, with a single species from Brazil; the Haplogleniinae, or “entire-eyed owlflies”, with ca. 100 valid species in 24 genera distributed in North and South America, western Asia, Africa and Madagascar; and the Ascalaphinae, or “split-eye owlflies”, with approximately 350 described species in nearly 75 genera, found worldwide. The Albardiinae are diagnosed as having entire eyes and antennae that do not reach past the origin of Rs in the forewing. The Haplogleniinae are diagnosed by having entire eyes and antennae that reach beyond the origin of Rs in the forewing. The Ascalaphinae, conversely, are diagnosed by the presence of a transverse, sulcus-like division across the eye, and by having antennae that reach beyond the origin of Rs in the forewing.

Because of their bizarre but charismatic appearance and unique biology, owlflies are a favorite group among entomologists. Nevertheless, they remain poorly understood. Characterizations of their biology are archetypal, with biological data having been described for fewer than a dozen species. Complete life histories have been published for fewer than half a dozen species. For most species, modern descriptions of adults are lacking, and the larvae are completely unknown. Most larvae cannot be identified to species, nor genus, nor even subfamily.

The family was last monographed by van der Weele in 1909. He treated 216 species and subspecies in three subfamilies, nine tribes, and 54 genera. In the years following van der Weele and prior to the work presented in this dissertation, new taxon descriptions had grown the family to its current size (ca. 450 species in three subfamilies, 15 tribes, and 100 genera), a nearly twofold increase in taxon representation at all taxonomic ranks except subfamily. This growth has pushed a new family-wide monograph nearly out of reach.

Almost all modern revisionary taxonomic works since van der Weele (1909) have been faunal in scope, with revisions having been performed on owlflies of the New World (Penny 1982a), the Amazon (Penny 1982b), Australia (New 1984), eastern India (Ghosh

1988), sub-Saharan Africa/Madagascar (Tjeder 1992), and Costa Rica (Penny 2000). These works have greatly improved our understanding of owlflies of these regions. However, none has interpreted the treated taxa within a modern phylogenetic framework, nor used phylogenetic methods to test the monophyly of the treated genera. Further, because they are faunal in nature, many of their identification keys do not include all known species in the genera they treat. And, most of them do not include illustrations of the male and female genitalia. Lastly, most ignore the issue of tribes, because the current tribal classification, which is based largely on van der Weele's (1909) ideas, is problematic. Van der Weele based his tribes on a few easily diagnosable diagnostic features, mostly of males. But several of these features, as they are characterized at the tribal level, seem to represent convergences, and thus the current tribal classification appears to recognize paraphyletic groups.

This dissertation updates knowledge of owlflies in two ways. First, it taxonomically revises six genera of Haplogleniinae, or entire-eyed owlflies, based on phylogenetic analyses of morphological characters. Second, it presents the first large-scale phylogenetic hypothesis for the family Ascalaphidae based on combined analyses of both morphological and molecular data. Specifically, the first two revisionary chapters (chapters II and III) complete Tjeder's (1992) posthumously published revision of the African Haplogleniinae, by treating his monobasic tribes Allocormodini (Chapter II, 11 species) and Tmesibasini (Chapter III, 10 species), the revisions of which he was unable to complete before his death. Chapter IV revises the Haplogleniinae of the Western

Hemisphere (37 species), a group demonstrated to be monophyletic in Chapter V. It tests the phylogenetic robustness of Penny's (1982a) generic characterizations, and presents a new classification for the group. Chapter V presents the first comprehensive phylogeny of the owlflies in the context of the suborder to which they belong, the Myrmeleontiformia. In so doing, it tests the traditional classification at all taxonomic levels, as well as the reliability of the diagnostic features (e.g., the entire vs. divided eye) on which the classification relies. The results will be critically important in future revisionary works that seek to restructure the classification of the family.

CHAPTER II

TAXONOMIC REVISION OF THE AFRICAN CRYPTIC-WINGED OWLFLY GENUS *ALLOCORMODES* MCLACHLAN, 1891 (ASCALAPHIDAE: HAPLOGLENIINAE)

Synopsis

The genus *Allocormodes,* a cryptically-patterned genus of entire-eyed owlflies (Haplogleniinae) broadly distributed across tropical sub-Saharan Africa, is revised. Eleven species are recognized, including five new species: *Allocormodes albus, Allocormodes inconspicuus, Allocormodes micheli*, *Allocormodes nigris*, and *Allocormodes nigristigma*. One species, *A. woodi* Esben-Petersen, is newly synonymized with *A. kolbei* van der Weele. All species are described and illustrated, and the first identification key to the species is provided. An hypothesis of intrageneric relationships based on a cladistic analysis of 35 morphological characters is presented.

Introduction

Allocormodes is a genus of entire-eyed owlflies (Haplogleniinae) that is distributed across sub-Saharan Africa from Guinea and Sierra Leone in the west to Kenya in the east, and as far south as northeastern South Africa. Several of its species are relatively large among owlflies (forewing lengths up to 48 mm), and all have more-or-less well-developed cryptic wing patterning. Despite its species having broad distributions and a striking appearance, the genus has not been revised in over a century, and no identification key to its species has ever been published.

The earliest-described owlfly species currently placed in *Allocormodes* is *Ascalaphus intractabilis*, which Walker (1860) characterized from material deposited in the British Museum. McLachlan (1871) first characterized the genus, erecting *Cormodes* to contain *intractabilis*. Taschenburg (1879) subsequently described the species *maculipennis*, which he placed in the genus *Haploglenius*. McLachlan (1891), who discovered that the name *Cormodes* was preoccupied (by *Cormodes* Pascoe 1861, in Coleoptera), proposed the replacement name *Allocormodes,* and included within it both *intractabilis* and *maculipennis.* The first and only complete revision of the genus was published by van der Weele (1909), who redescribed it and added three new species, bringing the total number to five. He did not, however, provide an identification key for the species. A single new species each was added to the genus by Navás (1925) and Esben-Petersen (1927). A half century later Tjeder began working to revise the genus as part of a comprehensive treatment of the southern African owlfly fauna (Mervyn Mansell, pers. comm.), but the portion of his work treating *Allocormodes* (see Tjeder 1992: 165) was never completed, and only parts of his work on African owlflies reached publication (Tjeder 1992; Tjeder & Hansson 1992). No manuscript materials from Tjeder's work on *Allocormodes* have been available for this study outside of type labels attached to several specimens by Tjeder. Tjeder's proposal to create a monogeneric tribe Allocormodini was published posthumously by his student C. Hanssen (Tjeder 1992: 165; see page 164 for an explanation), but little justification was provided for this tribe beyond the presentation of a short list of putatively diagnostic features. Tjeder's tribe Allocormodini is tentatively accepted here, but its scope and utility require additional consideration in the context of a broader assessment of haplogleniine phylogenetic relationships.

Materials and methods

Material

Owlflies in the genus *Allocormodes*, like most other nocturnal and crepuscular owlflies, are very infrequently collected, and are rare in natural history collections. This study is based on the examination of approximately 100 specimens borrowed from the following research collections. This list also includes collections from which specimens were not borrowed but which are referenced in this work. These are marked with an asterisk (*).

MSUC	A. J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan, USA
BMNH	The Museum of Natural History (British Museum of Natural History), London, UK
CAS	California Academy of Sciences, San Francisco, California, USA

CIRAD	Centre de Coopération Internationale en Recherche Agronomique pour Le Développement, Montpellier, France
CMNH	The Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA
EMUS	Utah State University Entomological Museum, Logan, Utah, USA
MFNB	Museum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany
MNHN	Muséum national d'Histoire naturelle, Paris, France
MHNG*	Muséum d'histoire naturelle, Geneva, Switzerland
NAVC*	R. P. Longinos Navás private collection
NMW	Naturhistorisches Museum Wien, Vienna, Austria
RMCA	Royal Museum for Central Africa, Tervuren, Belgium
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
UMSP	University of Minnesota Insect Collection, St. Paul, Minnesota, USA
USNM	Smithsonian National Museum of Natural History, Washington, D.C., USA
VDWC	H. W. van der Weele private collection
ZMH*	Martin-Luther-Universität, Zoological Museum, Halle-Wittenberg, Sachsen-Anhalt, Germany

Specimen examination

Both pinned and dissected specimens were visualized under a Leica MZ6 dissecting microscope enabling magnifications from 6.3 to 40 times.

Specimen preparation and dissections

Terminalia were prepared using the following methods: Two male and two female specimens of each putative species (morphotype) were selected for examination of their terminalia and internal abdominal structures. An effort was made to select specimens representing the range of morphological diversity seen for each morphotype (e.g., expressing variation in wing patterning or body/setae color), and to dissect type specimens (where available and permitted). Damaged specimens (e.g., broken, bearing fungus or excessive residues, eaten by dermestids) were avoided. In the case of type specimens, abdomens were cleaved at the posterior margin of the sixth segment using a sharp clean razor blade. This was done to retain as much of the original specimen in an unmodified state as possible. For all other specimens, the entire abdomen was removed by gently pressing it downward to break the narrower tissue immediately posterad of the metathoracic margin in the area of the foreshortened first segment.

Removed abdomens were placed in small plastic petri dishes containing a 70% solution of potassium hydroxide (KOH), and were left to macerate overnight at room temperature. Each petri dish was placed in a unit tray clipped to another tray containing the original specimen, in order to avoid association errors. Following digestion, abdomens were cleaned in 80% ethanol and further dissected. A single cut was made lengthwise along the right side of the abdomen from the base to the 8th segment through the soft pleural tissue, with an effort made to avoid cutting through spiracles. A transverse cut was then made near the posterior margin of the 8th segment to remove the terminal segments from the rest of the abdomen. Fine internal parts were flushed using a bent-tipped syringe to gently remove debris. Tracheae were removed from their spiracular attachments and discarded, and the midgut (crop and proventriculus) was separated from other tissues but retained. The crop and terminalia were flushed with ethanol to remove particulate matter and, in the case of many females, spermatophoric residues.

Specimens were then transferred to a fresh petri dish containing glycerin. Except for the crop, most tissues of interest were sufficiently sclerotized and pigmented to allow easy visualization via light microscopy, and thus were left unstained. At the conclusion of the project, all dissected parts were transferred to microvials and reassociated with their original specimens.

Photography and illustrations

Spread specimens used for habitus images were mounted on a Porta-Trace light table, and digitally captured with a Canon EOS 5D Mark II and Canon EF 24-70 mm 1:2.8 L USM Zoom lens. Certain microscopic features (e.g., leg setae, cleared genitalia, etc.) were digitally photographed at magnifications of 8–100x using a Leica M125 stereomicroscope with attached Leica DFC295 digital color camera, and were assembled using Leica Application Suite (LAS) software, which automatically captures and combines images at multiple z-axis levels in real time. Final images were processed in Adobe Photoshop. Line drawings were prepared with pencil and paper using a camera lucida attached to the Leica MZ6 dissecting microscope. Inked vellum copies were then digitally scanned and imported into Adobe Photoshop for cleanup and further processing. Wing illustrations were captured as digital color photographs and converted through a series of adjustments in Photoshop into dichromatic representations.

Terminology

Most of the anatomical terminology used here follows one or more of the following sources: Adams (1958), Aspöck et al. (1980), Penny (1982), New (1984), Tjeder (1992), or Nichols (1989). A number of new terms have also been created to facilitate the species descriptions. These are listed and explained below under ‘External adult morphology’.

Abbreviations and annotations

The following acronyms and abbreviations are used throughout (listed in alphabetical order): ATP, anterior tentorial pit; BIO, biology/ecology; DIS, comment, discussion or note; ET, etymology; FAL, femur anterolateral; FD, femur dorsal; FP, flight period; FPL, femur posterolateral; FV, femur ventral; FW, forewing; GD geographic distribution/collection record; GPC, gonarcus-paramere complex; H, habitat; HW, hind wing; IMS, immature stages [eggs, larval instars, pupa]; IS, some or all included species; JSYN, junior subjective synonym; K, key; masl, meters above sea level; MON, monograph; MOR, morphology; NN, new replacement name, nomen novum; OD, original description; RD, redescription [of senior synonym]; S1–S9, abdominal sternites one through nine; SR, specimen repository(ies); SYN, synonymical history; TAL, tibia anterolateral; TD, tibia dorsal; TGEN, type genus; TL, type locality; TPL, tibia posterolateral; TR, type repository; TSP, type species; TS, type specimen status; TV, tibia ventral; T1–T9, abdominal tergites one through nine. For acronyms and abbreviations pertaining to wings and wing venation see the Wings section of *External adult morphology*. Some additional abbreviations are introduced and defined in the individual figure captions where they are used.

Databasing

Each specimen examined for this study has been given an alphanumeric database number (i.e., JRJ_00000), and these numbers are referred to throughout this paper. The author's personal database in which these numbers are stored contains complete label data, GPS coordinates (as written on the label ["extracted"] or inferred from the label collection site data ["estimated"]), notes on specimen condition, notes from the literature regarding individual specimens, and other related data. Selected data pertinent to this revision are presented in Appendix 1: Excel file 1 (A1 Excel file 1).

The goal of the database presented in Appendix 1 is to: (1) allow for quick and easy side-by-side referencing of comprehensive specimen-level label, distribution and condition data; (2) provide the opportunity to rapidly and efficiently compare taxonomic concepts presented in descriptions created by the author with the exact specimens examined and used to formulate those concepts; (3) shorten species descriptions by removing extensive label data from the main text; and (4) facilitate future linking of other data associated with individual specimens, such as barcode numbers from other museum collections and molecular sequence data. The master database containing the *Allocormodes* dataset includes similar data for specimens of non-*Allocormodes* Ascalaphidae, other Neuropterida, other Insecta and other Arthropoda being examined for numerous ongoing projects by the author, and as such is dynamic and incomplete, being in a state of constant growth. It is maintained by the author, and as need requires, project-oriented subsets will be prepared for presentation and publication and thus be made publicly available. Information from the database is available upon request to the author.

External adult morphology

Because few authors have dealt specifically with the details of the morphological structure of adult ascalaphids, the following general morphological treatment will serve as an introduction to ascalaphid morphology, and as background for the detailed descriptions presented in the taxonomic treatments below. Asterisks (*) indicate terms and phrases that are newly proposed in this work.

Size

Allocormodes are medium- to large-sized owlflies, with forewing lengths ranging from 30–45 mm in males and from 33–48 mm in females. The two largest species, *A. intractabilis* and *A. lefebvrei*, have wing lengths approaching those of some of the largest owlflies in South America and Asia—e.g., *Haploglenius* spp., *Protidricerus* spp.—although *Allocormodes* abdomens tend to be much shorter than species in the latter genera. In general, females are larger than males, but in a few cases the sexes are essentially coequal in their dimensions (i.e., *A. kolbei*). Measurements for the body, including overall body length (head–abdomen) and length of the, abdomen, forewing, hind wing, and antennae, are recorded in Appendix 1 Excel file 2 (A1 Excel file 2).

Head

Occiput (A1 Fig. 4, *oc*). The surface is always glabrous and usually glossy, and bears various color patterns that are somewhat conserved in a few species but are often difficult to visualize because of the narrow space between the head and the thorax, or the poor quality or age of the specimen. In general, no characters of significant taxonomic value were found on the occiput.

Orbital sclerite (A1 Fig. 2, *aos*; A1 Fig 4, *pos* [=Tjeder 1992: 14, fig. 4, pos]). This narrow sclerite, also commonly referred to as the ocular rim, comprises the anterior orbital sclerite* on the front of the head and the posterior orbital sclerite on the back of the head (these transitioning conceptually at the vertex). It is consistently parallel-sided in species of *Allocormodes* and offset from adjacent sclerites (i.e., occiput, vertex, paraocular band) by a narrow sulcus-like depression, though on the front of the head this depression is usually absent or only weakly expressed. The sclerite is often concolorous with adjacent sclerites and is not of diagnostic value in this genus, as it is in some other genera (e.g., *Ululodes*).

Vertex (A1 Figs. 2, 4, *v*; 5, *lp*, *mp*). The vertex (*v*) bears a variety of textures and setae, which, if expressed consistently, might be of diagnostic value at the species level. Unfortunately, the patterns observed are highly variable both within and among species, and have not been found to be reliably diagnostic for species or groups of species. However, at the genus level, the pattern is broadly consistent: each side of the vertex bears three or four glabrous, slightly raised, triangular or rectangular lateral plates (*lp*) of yellow, orange or brown color, which adjoin the orbital sclerite and impose mesally upon the dark matte area that occupies the majority of the vertex. The matte texture of the latter area is created by a dense covering of fine microtrichia. From this dark region also often emanate long, erect, slender setae, although these are easily rubbed off in life or preservation and are often lost in museum specimens. In additions to the lateral plates, each side of the coronal suture is bordered parasagittally by a pair of narrow to broad, elongate, mesal plates (*mp*) of similar surface texture. The anterior plate is usually bifurcate near its posterior end in such a manner that its posterior terminals flank the anterior end of the smaller posterior plate. In some specimens the anterior plate consists of several small, aligned, pieces.

Prefrons (A1 Figs. 2, 3, *pfs*; =Tjeder 1992: 14, figs. 3, 6, pfr). Tjeder (1992: 15) proposed this term for the dorsal portion of the frons on which the antennae are mounted. In owlflies, this area is deeply angled into the head such that the antennal scapes, which emanate from the toruli (the sockets into which the antennal bases insert; singular = torulus), arise more-or-less dorsally from the head. In *Allocormodes*, the extent of the prefrons is not much larger than the toruli themselves; thus its shape is roughly similar to that of a transverse figure 8, particularly posteriorly. Tjeder delimited the posterior reach of the prefrons by the frontal arms of the epicranial suture; these arms, however, are not evident in *Allocormodes*. Instead, the posterior margin is evidenced merely by the inflection point where the plate transitions rapidly to the steep anterior portion of the vertex. The post-scapal portion of the prefrons is more readily visualized in specimens where the dense setae of the antennal bases do not obscure it. Tjeder (1992: 15) stated that the anterior margin of the prefrons is demarcated by a “deep horizontal suture-like inflection just below the toruli”. This corresponds with the anterior margins of the extra-torular sclerites (which Tjeder did not define; see below). Such a margin is a convenient place to demarcate the anterior limits of the prefrons in some owlflies, including *Allocormodes*, in which the extra-torular sclerites are broad and continue laterally to the paraocular bands and often have a distinct ventral margin; however, the extra-torular sclerites vary in the robustness of their development among other owlfly species, and their anterior margins are not always deep and ‘suture-like’. In *Allocormodes*, in fact, the inflection point where the frons transitions to prefrons is slightly ventrad of the extra-torular sclerites margins, albeit it rather smooth and poorly-defined. If the prefrons is margined by complete and distinct sutures only in certain cases, then it is conceptually useful to reinterpret it as the plane on which the toruli sit, delimited anteriorly and posteriorly by transverse inflections (to frons and vertex, respectively). In *Allocormodes* and many owlflies, then, the anterior portion of the prefrons is occupied principally, but not completely, by the extra-torular sclerites. A small portion of the prefrons rests anteromesally between the extra-torular sclerites, on the same plane.

Extra-torular sclerite* (A1 Fig. 2, *ets*). In owlflies, a transverse, raised band of sclerotized tissue borders each torulus anteriorly. This sclerite fuses mesally with its partner in a shallow sagittal invagination. In *Allocormodes*, the sclerites merge laterally with the paraocular band* (see below), and in some species the basal margin of the sclerites occasionally appear to express a weak sulcus. The sclerites are often paler in color than either the frons or the scapes. These sclerites appear to represent modified frontal (or, more specifically in the case of owlflies, prefrontal) tissue.

Paraocular band* (A1 Fig. 2, *pob*). The paraocular band is the continuous strip of sclerotic tissue on the face situated between the mesal sclerites (vertex, prefrons, frons, clypeus) and the anterior orbital sclerite. The dorsal margin of the band adjoins the vertex. In *Allocormodes* and most Haplogleniinae, the ventral margin is formed by the dorsolateral margin of the mandible base, which sits tangent to the anterior orbital sclerite. In Ascalaphinae and some Haplogleniinae (e.g., *Idricerus* and *Protidricerus*), the ventral margin is formed by the separate pleurostoma, a small triangular plate between the mandible base and the anterior orbital sclerite (see Tjeder 1992: 14, 15, fig. 6, pls). In many Ascalaphinae the ventral margin is formed by the subgenal suture. Some authors have referred to the paraocular band simply as the gena (e.g., Tjeder 1992: 14, 15, fig. 6, g; Michel 1998: 145). However, the band appears to be formed from the mesal part of the gena (ventrally), the lateral part of the frons (dorsally), and the anterior orbital sclerite (laterally). The band is distinguished here as a descriptively convenient region lying lateral to the frons-paraocular band inflection* (A1 Fig. 2, *fpi*; = clypeo-genal inflection of Tjeder 1992: 14, figs. 3, 6, clg) in which lies the elongate anterior tentorial pit (A1 Fig. 2, *atp*).

Posterior genal triangle* (A1 Figs. 3, 6). Posterad of the mandible base margin is a thin strip of tissue that sits adjacent to the ventral portion of the anterior orbital sclerite. It is often contiguous with, undifferentiable from, or obliterated by the anterior orbital sclerite, and is glabrous. In non-*Allocormodes* species with a broader paraocular band and/or a well-developed pleurostoma, the triangle is broader and dorsally margined by the ventral sulcus of the pleurostoma and/or the subgenal suture. The homology of the sclerite is unclear; it may be part of the postgena or hypostoma.

Labrum (A1 Figs. 2, 3, 7). The labrum is rather short and broad, transversely rectangular, with rounded ventrolateral angles; its length is approximately half that of the closed mandibles. Its ventral margin is weakly emarginated sagitally, and bears a fringe of long stiff curved setae, their apices directed toward the mandibles. The epistomal surface bears numerous short stiff setae; these are concentrated in two areas: (i) along the apical margin, where they are directed posterad and are somewhat appressed; and (ii) laterally, where they are directed mesad, and are shorter, more numerous, and more strongly appressed.

Mandibles (A1 Figs. 2, 3, 8–10). The mandibles are of typical owlfly form, being moderately short, robust, and triangular, with the apices curved mesad, and having the following additional general attributes: (i) each mandible is composed distally of a pair of thin blades, dorsal and ventral, separated by a mesal longitudinal excavation; (ii) the mesal margin of each of these blades constitutes the cutting surface of the mandible, and (iii), the cutting edge of the dorsal blade runs from the apex of the mandible to near its base, while that of the ventral blade runs from the mandible apex to ca. one half the length of the mandible.

In dorsal view (Fig. A1 2), the outlines of the two mandibles are approximately symmetrical, with the lateral margins evenly curved. The dorsolateral surfaces are glabrous, except for a few basolateral setae. The dorsomesal margins are concave, heavily sclerotized and apically acuminate. The basal portion of left dorsal blade has a notch (*n*) anterad to a short broad tooth (*lmt1*), while the right dorsal blade has a broad tooth (*rmt1*) at its base. In ventral view (Fig. A1 8), the mandibles appear quite asymmetrical, but each has modified forms of essentially the same features (see also A1 Figs. 9, 10): (1) a ventral face (*vf*) that terminates along the mesal margin in a cutting edge with a large tooth, (2) a mesal constriction, (3) a posteromesal setal fringe (*sf*), and (4) a posteromesal ridge (*pmr*). These features are explained further below. (1) *Ventral face*: in the left mandible, the ventral face is broad at its base and narrowed near its middle (the "mesal constriction"); immediately distad of the constriction is a cutting blade that expands mesally into a broadly triangular tooth (*lmt2*). The mesal margin of the blade between the tooth and the apex is concave and heavily sclerotized. In the right mandible, the ventral face is also broad basally, but narrows less medially. The mesal tooth (*rmt2*) of the cutting blade is longer and more acuminate than the corresponding left-mandible tooth. Distal to the mesal tooth, the mesal edge of the cutting blade is sharply angled and runs to the mandibular apex in a nearly straight line; this edge has very fine secondary crenulations in the form of minute shallowly curved cusps. (2) *Mesal constriction*: in the left mandible, this narrowing of the ventral blade corresponds with the mesal opening of a perpendicular excavation, or channel (*ch*), on the medial aspect of the mandible; dorsad of the constriction and the channel is, first, the distal reach of the posteromesal setal fringe (*sf*), second, the reinforced swelling of the posterior wall of the deep mesal groove which is visualized in ventral view as the posteromesal ridge (*pmr*), and third, the broad shallow pocket formed by the posterior portion of the mesal excavation (*me*). In the right mandible, the constriction is much shallower, and deepest immediately posterad of the second right mandibular tooth (*rmt2*); it corresponds to no specialized channels within the mesal excavation. (3) *Posteromesal setal fringe* (*sf*): in both mandibles, a fringe of setae running longitudinal to the long axis of the mandible arises inside the mesal groove immediately dorsad of the ventral face. The setae are in a narrow row, are slender but stiff, and decrease dramatically in length from the anterior to posterior limits of the fringe—the anterior-most setae are slightly longer than half the length of the ventral teeth, whereas the posterior setae are approximately only one-eighth this length. (4) *Posteromesal ridge* (*pmr*): in the left mandible, this heavily sclerotized swelling begins at the posterior wall of the mesal excavation and curves broadly and convexly toward the posteromesal margin of the mandible. In the right mandible, this ridge has become transformed into a medium-sized, sharply triangular mesal tooth (*rmt3*) with a narrow base, straight sides and a sharp apex.

Maxilla (A1 Fig. 11). The basicardo and disticardo are short and bear several long, very slender, setae. The stipes is stout and elongate; laterally it bears a fringe of long straight slender setae, which are longest basally and shortest apically. The palp is about as long as the stipes, with only the terminal two palpomeres extending beyond the apex of the galea. It is five-segmented; each palpomere except the ultimate bears numerous short stiff bristle-like setae. The galea is moderately elongate, somewhat flattened, with an apical brush of numerous elongate, stiff setae with mesally-curving hooked tips. The basigalea (Tjeder 1992: 15) is absent. The lacinia is short and broad, its mesal surface covered with numerous elongate, stiff setae with mesally-curving hooked tips, similar in form to those of the apex of the galea; the mesal margin of the lacinia also with elongate slender setae.

Labium (A1 Figs. 12, 13). The labium is often figured ventrally (Tjeder 1992: 15) but has notable features both ventrally and dorsally (interiorly). *Ventral features* (A1 Fig. 13). The submentum is broad and transverse, its surface convex and smooth, with numerous very long slender setae. The mentum also bears numerous very long slender setae. The palp is three-segmented, and is borne on a segment-like palpiger fused to the mentum. Each palpomere bears short stiff bristle-like setae, and the palpiger bears very long slender setae. The apical palpomere bears a subapical pore (*sp*). The ligula is emarginate distally and glabrous. *Dorsal features* (A1 Fig. 12). The ligula outline is horseshoe-shaped and bears a pair of broad, parallel, parasagittal tracks of dense, short, stiff setae. The setae are mostly directed mesad and distad, but those near and along the apical margin of the ligula are apically recurved proximad, toward the esophagous; the setae along the apical margin are the most stout and recurved. Otherwise, the dorsal surface of the ligula is glabrous.

Eyes (A1 Figs. 2–6). The eyes are entire and subhemispherical, slighter taller than long (A1 Fig. 3), and very slightly flattened posteriorly. The outlines of the ocular diaphragm and foramen orbitale (A1 Fig. 3) are circular.

Antennae. The antennae are comparable in length to those seen in other owlfly genera, reaching from about two-thirds (A1 Fig. 111) to approximately the entire distance (A1 Fig. 75) from the wing base to the pterostigma in spread specimens. The clubs are elongate pyriform (A1 Fig. 14). Parts of the antennae in several species bear setitori* (singular = setitorus; seta [Latin], 'bristle'; torus [Latin], 'round elevation, bulge'—A1 Fig. 15). These are slightly raised, sometimes oblique pimple-like structures that form the bases from which the setae emerge (similar swellings in Lepidoptera and Chrysopidae are called chalazae, but homology with the setitori in *Allocormodes* has not been established and a new term is preferred). In species where this feature is well-expressed, these bumps are often darkly colored, and increase in density distally along the flagellum. In at least one species the setal spots are present while the swellings are absent. Similar colored spots are also seen on the integument at the bases of setae on the legs of many species. All species have at least several verticils on the basal flagellomeres, and most species have at least some small setae along the length of the flagellum, but in some species, the mesal flagellomeres are virtually glabrous.

Thorax

Dorsal cervical plates* (A1 Figs. 3, 5, 16). A pair of sclerotized, elongate, knob-like plates that are situated in the dorsal membranous tissue of the cervix. They are hidden, or nearly so, when the head is flexed upward or if the cervix is damaged.

Cervical sclerite (A1 Figs. 17, 18). The lateral membranous tissue of the cervix bears a pronounced postero-ventrolaterally directed plate that terminates in a rounded knob. The posterior surface of the knob lies appressed to the lateral anterior margin of the proprescutum. The knob's color is more-or-less conserved within species and thus is useful as a diagnostic feature. It usually bears long subapical setae.

Ventral cervical plates* (A1 Fig. 3, 17). These plates, situated in the ventral membranous tissue of the cervix, are similar to the dorsal cervical plates but are slightly smaller and usually more round. They are difficult to see when the head is flexed downward or if the cervix is damaged.

Pronotum (A1 Figs. 5, 16, 18). In all owlflies the prothoracic somite is strongly narrowed and reduced longitudinally with very simplified notal morphology. In a few genera, including *Allocormodes*, the pronotum is slightly longer and has relatively well-developed morphology. Tjeder (1992: 18, 19, figs. 28, 29) observed that the notal sclerites in these genera bear a strong resemblance in shape and position to the major sclerites of the meso- and metanotum, and, accordingly, used for them the terms 'prescutum' and 'scutum'. But such usage implies a notion of serial homology that is almost certainly incorrect. Snodgrass (1935: 172–183) explained that external shape of the tergal plates of the pterothorax reflects internal phragma and flexion lines associated with musculature used in flight. Thus, they "have no relation to those characteristic of the wing-bearing terga" (Snodgrass 1935: 172). New terminology is here proposed to describe the pronotal features in owlflies. There are three narrow, transverse regions of the owfly pronotum. The anterior-most region, which forms the pronotum anterior margin, is raised into an often-bilobed transverse rim, the anterior flange* (Tjeder's 'prescutum'). The flange is sometimes divided by a sagittal sulcus, and it varies in development from very thin, with approximately parallel anterior and posterior margins, to more robust, with well-developed left and right sublateral lobes. In *Allocormodes* it is narrow and flange-like and only weakly bilobed, being separated by a thin sagittal sulcus. The second region is the most consistently-expressed pronotal feature in terms of shape, the medial transverse band*(A1 Figs. 16, 18, *mtb* [Tjeder's 'scutum']). This portion of the notum is longitudinally very short, and sometimes further narrowed sagittally. It is produced along the lateral reaches of the sclerite into the posterolateral knob* (A1 Fig. 18, *plk*), but it is otherwise undeveloped. The posterior region of the notum, in *Allocormodes* and most owlflies, is narrow and rim-like, and is here called the posterior flange*. In some South American and African genera this flange is well-developed into an articulated valve (see Chapter 3).

Mesothorax (A1 Figs. 16–18). This is the largest somite of the body; it contains the bulk of muscle tissue necessary for powered flight in owlflies. Dorsally, it has a well-developed prescutum, scutum and scutellum. The prescutum is sagittally divided by a longitudinal sulcus. The scutum bears, anteriorly, a pair of usually conspicuous velvety spots. The scutellum is transversely depressed medially. Posterad of these well-developed regions are a narrow subscutellum and a bilobed postnotum. The mesothoracic pleuron is subdivided into many plates; the largest of these, the anepimeron, is invaded dorsally by a conspicuous, triangular, membranous region, the mesothoracic subalar membrane*.

Metathorax (A1 Figs. 16–18). Considerably smaller than the mesothorax, the metathorax possesses most of the same sclerites. The metathoracic prescutum, which lies immediately posterad of the mesothoracic postnotum, in *Allocormodes* is secondarily divided anterolaterally by oblique inflections, these sometimes expressed as thin sulci.

The offset anterolateral regions are transversely elongate and triangular or quadrangular, and are here called the paraprescutum* (A1 Figs. 16, 18, *pps3*); they are also sometimes differentially colored from the prescutum. The scutal lobes are separate from one another (i.e., not contiguous sagittally) and positioned laterally, and on their anteromesal surface have a rough texture for receiving the ventral gripping microtrichia of the anal angle of the forewing. The postnotum is absent. The pleuron is similar to that of the mesothorax, but the subalar membrane does not extensively invade the anepimeron.

Legs

As in most owlflies, the legs of *Allocormodes* are rather short and stout, often multicolored, with elongate five-segmented tarsi and numerous and diversely structured and colored setae.

Color. Integument coloration often varies from leg to leg, both within and among species. In paler species, leg coloration often includes dark spots on the integument at the bases of some setae (A1 Fig. 19).

Setae. Among species, and among leg pairs, setae vary in many characteristics, including thickness, length, color, and density—for example, the antennal comb vs. the long, stiff, filtering setae of the prothoracic tibia (A1 Fig. 21)—and an efficient way of characterizing and referencing these varations becomes necessary. For convenience, the femur and tibia are treated as if they have four surfaces, arranged around each segment as illustrated in A1 Fig. 21. The surfaces that are opposed when the leg is flexed are treated as 'ventral'. The opposite surfaces are 'dorsal', regardless of their position or orientation of the leg with respect to the body. When the leg is held perpendicular to the longitudinal body axis, the surface facing anteriorly is treated as 'anterolateral', and the opposite surface is 'posterolateral'. A set of corresponding acronyms for these surfaces is given above in '*Abbreviations and annotations*'. It should be pointed out that this is a convention of convenience—the leg segments are actually subcylindrical, and often the setae of a particular form do not occupy only one of the designated surfaces, but occupy parts of adjacent surfaces. For descriptive purposes, if the same form of setae occupy extensive parts of multiple (usually adjacent) surfaces, then the same setal description is applied to each. But where overlap onto adjacent surfaces is small, the setal description is applied only to the major surface on which is occurs. Where a surface is prominently characterized by multiple setal forms, each form is noted. The term 'mixed' is used to refer to different setal forms that are intermingled on the same surface.

Wings

Venational theory and nomenclature. The evolution of wing venation across the superorder Neuropterida has been explored by Martynov (1924), Carpenter (1940), Adams (1958) and others, each, in turn, building both upon one another's ideas and upon concepts developed for the broader Pterygota by Comstock and Needham (Comstock

1918), Tillyard (1919), Lameere (1922), Martynov (1930) and others. A useful review of the literature and a discussion of the progress of venation theory for the Neuropterida are given in Adams (1958).

Wing venation evolution across the Ascalaphidae has not yet been evaluated in depth. However, a theoretical framework and system of nomenclature for the major veins in the Osmyloidea, a superfamily proposed by Adams that contains the Ascalaphidae, was developed in his unpublished doctoral dissertation (1958). The Osmyloidea, sensu Adams, although not supported as monophyletic in recent phylogenetic studies (see for example Aspöck and Aspöck 2008 and Winterton 2010), contains most of the same families as the much earlier proposed and now well-supported Myrmeleontiformia (= Psychopsidae + Nymphidae + Nemopteridae + Myrmeleontidae + Ascalaphidae; see review of literature and synapomorphies in Winterton 2010), but excludes Psychopsidae and includes both Osmylidae and the extinct family Nymphitidae. In spite of the more recent restructuring of phylogenetic hypotheses regarding relationships among these families, Adams' fundamental notions and terms are still useful, and more-or-less have been accepted and adopted by the Neuropterological community at large (see, for example, Stange 1970, Aspöck et al. 1980, and Mansell 1985), and applied, although with some inconsistency, to the Ascalaphidae (e.g., Aspöck et al. 1980; New 1984; Tjeder 1992).

A comparative study of the wings of selected members of Myrmeleontiformia was performed separately (unpublished data). Conclusions drawn from that investigation form the basis for the ideas presented here regarding the genus *Allocormodes*.

In *Allocormodes*, and many owlflies, the basal corrugation and layout of the venation of the fore- and hind wings appears superficially extremely similar. However, one result of Adams' work was to establish that some of the longitudinal veins inclusive and posterad of Mp, while present in both wings and homologous in origin, are different in position, fusing or branching. Thus, the terminology of these posterior veins is in some respects non-intuitive between the two wings. The nomenclature used here is given in A1 Figs. 22–25 and should be consulted when reading descriptions of owlfly wings. A detailed explanation of the veins and wing areas recognized here follows.

Wing venation

<u>Veins vs. veinlets vs. crossveins</u>. In this work, the term <u>vein</u> refers to any of the major longitudinal veins that originate at or near the wing base or that fork from a major longitudinal vein and then continue for a considerable distance, usually along the long axis of the wing (the anal veins, some of which are quite short, and a few veins which secondarily fuse with other veins, i.e., Mp_2 in the forewing, are exceptional). The major longitudinal veins are the costa, subcosta, radius, radial sector, media, cubitus, and anal veins. These veins, and their various branches and fusions, are diagrammed in A1 Figs.

22, 24 and 25. Their specific names and abbreviations are given in '*Abbreviations and annotations*', above, and described in more detail below. Veinlets are short pieces of veins that originate and are part of longitudinal veins, generally near the wing margin. The term is particularly applied to the 'subcostal veinlets' (rather than 'costal crossveins') that branch anteriorly from the subcosta and run to the wing margin in the costal area. Veinlets are distinguished here from crossveins, which typically join elements of veins and veinlets, usually at approximately right angles, but may, in some wing areas, also join other crossveins. See Oswald (1993) for additional information and context regarding the differences among these three types of venational elements.

Convex vs. concave veins. The base of the neuropteran wing is distinctly corrugated, with some longitudinal veins occupying a concave (elevated) position and others a convex (depressed) position. Adams (1958) observed that while this feature is important in understanding wing evolution, most works that include wing illustrations and discussions do not point out whether individual veins are concave or convex. For the benefit of possible future studies on the evolution of wing venation in the Ascalaphidae, veins are designated below as convex or concave (A1 Fig. 22).

Forewing veins

Costa (C). A simple convex vein circumscribing the entire wing. The portion of the costa along the posterior margin of the anal area and distad of the axillary cord is termed the ambient vein (see Tjeder 1992: 25, figs, 25, 36–40).

Subcosta (Sc). A robust concave vein originating at the base of the wing and continuing to wing margin after fusing with R in the pterostigmal area to form Sc+R. The portion of Sc fused with R represents the posterior subcostal trace (sensu Oswald 1993a), as opposed to the numerous branches (subcostal veinlets) which arise from Sc+R in the apical area.

Subcostal veinlets (scv). These veinlets arise anteriorly from the subcosta and run to the wing margin within the costal and apical areas. They are generally unforked in *Allocormodes*, proximal to the pterostigma, but often singly or multiply branched distal to the pterostigma.

Recurrent vein (rv). In many neuropteran families, the first subcostal veinlet, or humeral veinlet (*hv*), recurves toward the body to strike the costa close to the wing base, often with several branches that reach the costa. In *Allocormodes*, as in all owlflies examined thus far, this veinlet is unbranched, slightly recurrent, and straight.

Radius (R). A robust convex vein, R originates at the base of the wing and continues to the wing margin after fusing with Sc in the pterostigmal area. A single branch, the radial sector, forks posteriorly from the radius in the proximal portion of the wing. The undifferentiated anterior branch continues straight to fuse with Sc in the pterostigmal area, and represents the anterior radial trace (sensu Oswald 1993a).

Radial sector (Rs). A concave vein for a short distance after its separation from R, originating somewhat distant from wing base (at approximately one-fourth total wing length), then continuing to wing margin. Forked two or more times, with numerous crossveins and veinlets connecting its branches within the radial area (see discussion for Radial area). The first branch is Rs_1; near its origin on R it is flat or somewhat depressed on the wing plane, but in its distal half it becomes a convex vein. In all *Allocormodes*, and many species of owlflies, the next branch, Rs_2, runs closely and parallel to Rs_1, and is a concave vein. Where Rs_2 strikes the wing margin, the margin is often slightly emarginate.

Media anterior (Ma). Martynov (1924), Carpenter (1940), and Adams (1958) have discussed in great depth the evolution of wing venation in Neuropterida. Of particular interest is the evolution of the media, which in many non-neuropterid insect lineages has predominant anterior and posterior branches. Adams (1958) concluded that within the Osmyloidea Ma was sometimes present in the forewing as a vestigial crossvein-like vein, which he labeled the basal piece, or ‘b’ in his diagrams. However, he provided little hard evidence for this conclusion, and some subsequent authors (e.g., Oswald 1993a; Yang et al. 1999; Makarkin et al. 2013) have argued that ‘b’ represents crossvein 1r-m, not Ma. Based on personal examinations of representatives of each of the myrmeleontiform families, and Hemerobiidae and Polystoechotidae, there interpretation adopted here is that early in the Myrmeleontiformia, or possibly even earlier within the Neuropterida, Ma ceased to be expressed, and that the ‘b’ vein of Adams is 1r-m. In the Nymphidae, Myrmeleontidae and Ascalaphidae, 1r-m is secondarily oblique and a very robust convex crossvein; in Psychopsidae and Nemopteridae it is only weakly oblique and slender. Crossvein 1r-m is present in *Allocormodes*, as apparently in all Ascalaphidae.

Many authors (e.g., MacLeod 1971, Aspock et al. 1980, etc.) have followed Adams in labeling the first posterior branch of the radius Rs+Ma. Such convention is not followed here; rather, the first branch is referred to simply as Rs, and serial posterior branches of Rs are designated as Rs_1, Rs_2, etc. (A1 Fig. 22).

<u>Media posterior (Mp)</u>. A well-developed concave vein, it forks early at about one-fourth the distance from the wing base, with the posterior fork (Mp_2; see below) crossvein-like and running to Cua_1.

Anterior branch of media posterior (Mp_1). Distal to the Mp fork, Mp_1 continues to wing margin as a simple longitudinal vein. As with Rs_2, where Mp_1 strikes the wing margin the margin is often slightly emarginate.

Posterior branch of media posterior (Mp_2). Distal to Mp fork, Mp_2, which is short and crossvein-like (the oblique vein, 'o', of Adams 1958), immediately fuses with Cua_1, and continues as Mp_2+Cua_1, a convex vein, to the wing margin, closely paralleling Mp_1.

Cubitus (Cu). A convex vein, the Cua forks close to the wing base into Cua and Cup. Crossvein 1m-cu is very robust, strongly oblique, convex, and closely aligned with crossvein 1r-m to form, with adjacent elements of the Mp, a distinct basal chiasma*.

Cubitus anterior (Cua). A very robust convex vein which forks at a point approximately one sixth the distance of total wing length. The anterior branch of the fork, Cua_1, fuses after a short distance with Mp_2. The posterior branch, Cua_2, angles sharply toward the posterior margin of the wing, but its terminus on the margin is obscure, as in most owlflies. In *Allocormodes*, the terminus is lost among the marginal cells, discussed below.

Cubitus posterior (Cup). The Cup branches from the cubital stem immediately distad of the cubital end of 1m-cu. Following a short curve, Cup straightens and runs obliquely toward the wing margin. Along this run, often near its midpoint, it fuses with 1A to become Cup +1A. Near its terminus, Cup+1A appears to fuse with Cua_2 and is subsequently lost in the marginal cells. Thus the exact terminus of the Cup on the posterior wing margin is usually unclear.

First anal vein (1A). A moderately robust concave vein, it closely parallels the base of Cup before fusing with it, and, as Cup +1A, continues toward the wing margin where it further fuses with Cua_2.

Second anal vein (2A). A relatively short and robust convex vein, 2A fuses with 3A very close to the wing base to become 2A+3A. 2A+3A, also a convex vein, then appears to diverge again into separate 2A and 3A veins, both of which then divide into webs of vein elements that are impossible to uniquely assign as anal veinlets or crossveins.

Third anal vein (3A). See ‘Second anal vein (2A)’, above.

Hind wing veins

Costa (C), Subcosta (Sc), Subcostal veinlets (scv), Radius (R), Radial sector (Rs). As in the FW.

Media anterior (Ma). Several families of Neuropterida (e.g, Polystoechotidae; but none in the Myrmeleontiformia) display a sigmoidal veinlet that originates near the base of M and fuses anteriorly with the base of R or Rs. This "sigmoid vein" has been interpreted by some, including Adams (1958), to represent the base of Ma. In all Ascalaphidae, including *Allocormodes*, this veinlet is absent, and there is no other evidence of fusion of Ma with R. The hind wing Ma is herein interpreted to be completely absent in *Allocormodes* (and in all other owlflies).

<u>Media posterior (Mp)</u>. A well-developed concave vein, Mp forks extremely close to the wing base into Mp_1 and Mp_2.

<u>First branch of media posterior (Mp_1)</u>. A robust concave vein as in the forewing, Mp_1 continues to the wing margin as a simple longitudinal vein. As with Rs_2, where it strikes the wing margin the margin is often slightly emarginate.

<u>Second branch of media posterior (Mp_2)</u>. This robust convex vein forks from the Mp stem near the wing base. Unlike the condition in the forewing, Mp_2 is not crossvein-like and does not fuse quickly with Cua_1 (although Mp_{2p} does fuse with Cua at its terminus). In form, the hind wing Mp_2 strongly resembles Cua_1 of the forewing. Both are convex veins, both branch in similar areas, and both have similar shapes and positions of their branches. A careful examination of the origins of the major longitudinal veins at the fore- and hind wing bases and a comparative analysis of the same in other families of the Myrmeleontiformia, however, reveal the probable sequence of evolution that led to the convergence of wing topology in the fore- and hind wings of *Allocormodes*. In

Stilbopteryx and *Albardia,* for example, a well-developed hind wing Mp_{2p} vein (resembling the forewing Cua) is lacking, suggesting that the differentiation of a well-developed hind wing Mp_2 fork likely occurred after the evolution of those two groups. In addition, the convexity/concavity of the Cu veins of the fore- and hind wings are not equivalent to those observed in Nymphidae. In *Allocormodes* and most owlflies except the Ululodini, Mp_2 forks prominently at a point approximately one sixth the distance of total wing length, into Mp_{2a} and Mp_{2p}.

Anterior trace of second branch of media posterior (Mp_{2a}). Distal to the Mp_2 fork, the anterior branch continues as Mp_{2a}, a convex vein, to the wing margin, closely paralleling Mp_1.

Posterior trace of second branch of media posterior (Mp_{2p}). From the Mp_2 fork, the posterior trace, a convex vein, angles sharply toward the posterior margin of wing, but its terminus is lost among the marginal cells and is obscure.

Cubitus anterior (Cua). The Cua, a concave vein, runs parallel to Mp_2 before curving posterad to run subparallel to Mp_{2p}. Its terminus either fuses with Mp_{2p} or is lost in the marginal cells.

Cubitus posterior (Cup). The Cup, a convex vein, fuses with 1A very near the wing base, and, as Cup+1A, runs parallel to Cua for most of the latter's length. Cup+1A does not have a well-defined terminus, as it generally branches into a field of weakly differentiated veinlets and/or crossveins in the anal area.

First anal vein (1A). This convex vein fuses with Cup very near the wing base and continues as Cup+1A to the posterior wing margin.

Second anal vein (2A). 2A fuses with 3A shortly after its origin from the wing base. It then separates again after a short distance and either curves anterad to fuse with Cup+1A, or curves posterad to strike the posterior wing margin.

Third anal vein (3A). This robust convex vein fuses with 2A shortly after its origin, then diverges and curves abruptly posterad to strike the posterior wing margin.

Wing regions

Area* vs. domain* vs. triangle*. It is frequently convenient to be able to efficiently reference particular wing regions in order to locate their attendant venational elements, cells, maculation patterns, or other phenomena. To provide a standard framework for the localization of various wing structures, the wing is here divided into a set of mutually exclusive areas, some of which are further partially subdivided into domains or triangles. The term "area" will refer to a region of the wing whose borders are delimited by major longitudinal veins, the wing base, and/or the wing margin. "Domains" and "triangles" are parts of areas that are specially defined because of unique features or descriptive convenience. Each of the areas, domains and triangles used herein is defined and discussed below, in alphabetical order. A few special cells are also discussed.

Glossary of regions

Anal area [FW and HW]. This area is delimited proximally by the wing base, anteriorly by 1A/Cup+1A (forewing) or Cua (hind wing), posteriorly by the posterior wing margin, and distally by the proximal-most marginal cell.

Anterior medial area [HW only]. This area is bound proximally by the wing base, anteriorly by Mp_1, posteriorly by Mp_2/Mp_{2a}, and distally by the wing margin, and is the analog of the mediocubital area of the forewing.

Apical area* [FW and HW]. Called the “apical field” by New (1984) and Tjeder (1992), this area is bounded by the distal-most aggregated pterostigmal veinlet (rather than the distal reach of pterostigma pigment, which is highly variable in owlflies), the wing margin, and Sc+R, which, distal to the anastomosis of Sc+R curves strongly posterad, approximately paralleling the contour of the anterodistal margin of the wing. The apical area contains several branched and unbranched subcostal veinlets which are often connected by numerous crossveins. In some cases the irregularity of the veinlets and crossveins causes much of the area to appear reticulate. Apical area veinlet counts include only veinlets that are not partially overlapped by pterostigmal pigment. Apical area crossvein counts include those occurring on both sides of all apical area veinlets and their branches.

Compressed marginal domain (cmd)* [FW and HW]. This domain is located along the wing margin in the distal portion of the radial area. It is rectangular in shape and consists of several rows of cells that are distinctly smaller than cells in adjacent rows. The lateral-most rows often appear to be convex toward the center of the domain, giving the domain a squeezed or compressed appearance. The veins within the domain are often pale yellowish or white. The domain is often incorporated into the apical pigment patch found in the forewings of male *Allocormodes*, and its membrane may bear white pigment. This feature is not unique to *Allocormodes*, having also been observed in the closely-related genus *Campylophlebia*.

Costal area [FW and HW]. This area is circumscribed anteriorly by C, posteriorly by Sc, and distally by the proximal-most aggregated pterostigmal veinlet. In *Allocormodes*, the shape of this area in the hind wing is diagnostic for groups of species.

Cubital area [FW only]. The cubital area is defined proximally by Cua_2, anteriorly by Cua_1/Mp_2+Cua_1, and posteriorly by the hind margin of the wing.

Cubital triangle* [FW only]. This area is delineated anteriorly by Cua, posteriorly by Cup/Cup+1A, and distally by Cua_2. Cua_2 and Cup+1A rarely join to close the triangle acuminately, but usually remain slightly separated and connected by a short crossvein, giving the triangle a blunt apex. This truncation sometimes adjoins one or more triangular or quadrangular marginal cells (see 'Marginal cells', below), but frequently is separated from them by a short marginal crossvein.

In *Allocormodes*, the cubital triangle varies in size, usually correlating with the overall size of the specimen and thus the wing. Larger species often have larger triangles with greater numbers of veinlets, crossveins and cells. The basal portion of the triangle (proximal to the cubital fork) is crossed by several usually unbranched crossveins, although these may be interconnected by one or more additional crossveins near the fork. The portion of the triangle distoposterad of the fork and before the apex is referred to as the distal domain (dd)*. This domain is crossed by one to several crossveins, but these are often not parallel to one another and are often interconnected by other irregular crossveins, forming a set of irregular cells. For the sake of simplicity the contents of this area are characterized in this work in terms of the approximate number and/or shapes of the cells, rather than number of crossveins. The first cell counted in descriptions is the (usually large) one bordering the cubital fork, even though a portion of it may extend basad of the fork itself.

Hypostigmatic cell [FW and HW]. In Nymphidae and most Myrmeleontidae a second radial sector forks posterad from R in the distal portion of the wing near the pterostigma (see, for example, Aspöck et al. 1980: F 211, F 220). Distad of this second radial sector is the hypostigmatic cell, a narrow and greatly elongate cell subtending R and proximal portion of Sc+R. In *Allocormodes* and other Ascalaphidae the second radial sector is indistinguishable from adjacent r-rs crossveins, and the hypostigmatic cell it is not differentiated in size from adjacent cells. Comparative analysis of putatively basal lineages of antlions and owlflies (*Palpares*, *Stilbopteryx* and *Albardia*) suggests that over time the second radial sector gradually oriented itself perpendicular to R to resemble other adjacent crossveins, and the hypostigmatic cell gradually shortened and/or subdivided into many smaller cells by the addition of new crossveins.

Marginal cells* [FW and HW]. The marginal cells constitute those cells whose anterior margins adjoin the distal margin of the cubital triangle (forewing) or medial triangle (hind wing) and whose posterior margins lie along the wing posterior margin, and who cannot be confidently assigned to either the anal or cubital (forewing)/posterior medial (hind wing) areas. The numbers and shapes of the cells vary intraspecifically and even from wing to wing in the same specimen. In *Allocormodes* the cells are triangular or quadrangular (or possess even more sides—see hind wing in Fig. 26), and may be singular or occur in sets or two or more (specimens have been observed with sprays of up to five narrow cells—see Fig. 56, right hind wing). Sometimes the marginal cell is separated from the distal domain by a short crossveins (Fig. 26, forewing). In some other genera of owlflies the marginal cell(s) may be broad, secondarily divided transversely into two or more cells, and appear as an extension of the distal domain.

Medial triangle* [HW only]. Analogous to the cubital triangle of the forewing, but differing in being delimited proximally by the wing base, anteriorly by Mp_2, posteriorly by Cua, and distally by Mp_{2p} and the marginal cells. It is usually more slender than the cubital triangle, and its posterior margin (Cua) more strongly curved. It is also usually longer and more slender with more distal cells in males, and shorter and more robust with fewer distal crossveins in females. The veinlets of the fork area itself are sometimes branched or connected by a crossvein or two, but veinlets past the fork (in the distal domain), if present, are unbranched and can be counted easily. The distal domain is as in the cubital triangle, and in *Allocormodes* is generally well developed, with several cells. The contents of this domain are characterized as in the forewing. In one species (*A. lefebvrei* van der Weele), and in some species in other genera of owlflies, the distal domain may be reduced to just a single cell or may be absent altogether. This often occurs in species with narrowed wing bases. As in the forewing, post-triangle cells are referred to as marginal cells.

Mediocubital area [FW only]. This narrow area is delimited proximally by the wing base, anteriorly by Mp/Mp_1, posteriorly by $Cua/Cua_1/Mp_2+Cua_1$, and distally by the wing margin.

Posterior medial area [HW only]. The posterior medial area is defined proximally by Mp_{2p} and the distal-most marginal cell, anteriorly by Mp_{2a}, and posteriorly by the hind margin of the wing. It is analogous to the forewing cubital area.

Postsectoral area [FW and HW]. This area is delimited proximally by the first rs-m crossvein, anteriorly by the posterior-most sectoral trace, posteriorly by Mp_1, and distally by the wing margin.

Presectoral area [FW and HW]. This area is delimited anteriorly by R and sometimes a small part of the base of Rs, posteriorly by Mp, and distally by the first rs-m crossvein.

Radial area [FW and HW]. This area is delimited anteriorly by the anterior radial trace and Sc+R, posteriorly by the posterior-most sectoral trace, and distally by the wing margin. The region contains the compressed marginal domain as a subarea.

Subcostal area* [FW and HW]. This is the very narrow area delimited by the wing base, subcosta, and radius/anterior radial trace. In most owlflies, this area is devoid of subcostal crossveins (scc). In a few species of *Allocormodes*, the distal half contains a series of often irregularly spaced transverse crossveins.

Wing maculation

Wing patterning. The maculation pattern in *Allocormodes* is quite distinctive and diagnostic for the genus, and is described in detail in the formal genus description. As it seems to visually break up the ouline of the wing, it presumably serves a camouflage function, obscuring the imago as it rests on some substrate. By virtue of its conspicuousness, this pattern forms the basis for the common name proposed here for the genus, the African cryptic-winged owlflies.

Pterostigma. In *Allocormodes*, the pterostigma is highly variable in color and size, even within species. Determining the properties of the pterostigma for descriptions requires an understanding of its components. A careful examination of the pterostigma reveals that it consists of two primary elements: (1) a series of closely arranged subcostal veinlets; and (2) pigmentation that varies substantially in several qualities.

(1) Veinlets. The pterostigma encompasses approximately 1–4 subcostal veinlets proximal to, and another 1–4 veinlets distal to, the anastomosis of Sc+R. These veinlets are usually parallel or slightly divergent with respect to each other and may be either more-or-less evenly, or differentially spaced. One or more crossveins are often forked, often near where they originate from Sc or Sc+R, but sometimes closer to the wing margin; occasionally forked veinlets branch again (twigging). Only very rarely are there crossveins joining the veinlets, and these appear to be adventitious.

(2) Pigmentation. Color is expressed in two palettes, each with its own associated formational artifacts. The first palette is a set of "cream" colors. This pigment may be nearly white, yellowish, or slightly orange, but is usually a yellowish white. When fully expressed, it is absolutely opaque and may completely fill cells. When weakly expressed, it may tinge only the center of a cell; otherwise it occurs as a very pale hue of whitish, amber yellowish, slight orangish or even brownish evenly distributed over entire cells. Color may even be completely lacking, but the presence of the cream pigmentation process is almost always observable as an obscuring of the transparency of the membranes. The second palette is a set of dark red to nearly black pigments that are most frequently dark reddish brown. These have a different quality in that they are formed as aggregates of fine granules imbedded in the wing membranes, often the same membranes that bear cream pigment. These aggregates may organize as mesal patches in the center of the wing membrane cells, or they may margin the cells. Often they do both, merging and combining to fill cells partially or completely. From a distance the granules appear merely as continuous dark pigment. When very dense, they render pterostigmal membranes opaque with an effect similar to that of the cream pigment.

Apical pigment patch (A1 Fig. 78). In males of most *Allocormodes* species, the forewing apex bears a patch of opaque, pure white pigment. Thus, it is usually very easy to sex specimens without examining terminalia. The character of this coating is different from the cream and dark pigments discussed under pterostigmal pigmentation. The patch is formed from a thin, chalky but rigid, white coating born on the ventral surface of the membranes. The layer is glaze-like and may or may not be waxy (it seems to be more-or-less insoluble when exposed for a few minutes to 80% ethanol, but is easily abraded when scratched with a minutin pin). More intensive examinations, by scanning electron micrography or other techniques, are needed to determine its true attributes. A few species lack the pigment layer, but exhibit very pale yellow or whitish veins, veinlets and crossveins in the same wing area. There does not appear to be a correlation between increased density of pigment and increased specimen age—younger specimens (those retaining coronal and thoracic setae and with less wing damage) seem to express the pigment most densely. No vestige of pigment is found in the forewings of females in the area of the patch. As with the compressed marginal domain, this feature is seen in the related genus *Campylophlebia*.

<u>Melanism</u> (A1 Figs. 66, 68, 105). Males of several species of *Allocormodes* sometimes exhibit extreme darkening of the wings. This darkening consists of increased margining to complete pigmentation of wing cell membranes, and may or may not obscure other patterns that may be readily seen in non-melanistic individuals. The reasons for this melanism are unknown. They may be environmental or genetic or both, and it has been suggested that darkening may increase in individuals over their lifetime, but this has yet to be demonstrated. Too few specimens are currently available to draw any conclusions as to whether the phenomenon may be population specific, and/or have a geographic component. Melanism has not yet been observed to occur in females of *Allocormodes* and seems to be a male-specific trait.

Abdomen

Male and female abdomens in *Allocormodes* (A1 Figs. 27, 28) are similar in size and shape, unlike in many other genera of owlflies. Coloration is brown or grayish, and mostly unremarkable in dry pinned material. There are no distinct patterns on either the tergites or sternites beyond the paleness of the posterior margin of each segment (in specimens of many species); however, several species do have the integument of tergites 1–3 or 1–4 rather pale or cream-colored (in both males and females). Setal tufts are essentially absent, although several species bear variously dense pleural setae on segments 1–3.

<u>Male terminalia</u> (A1 Figs. 27, 29, 31). The gonarcus and parameres together form a sclerotized, acorn-shaped structure, the gonarcus-paramere complex, or <u>GPC</u>*, which is situated within the genital cavity above the 9th sternite and below the unproduced ectoprocts. The gonarcus, which is the upper hemisphere of the complex, is more-or-less completely sclerotized. The paired parameres (=9th gonocoxites in other Neuropterida, e.g., Psychopsidae—see, for example, Oswald 1993b), which form the ventral hemisphere of the complex, cradle each side, their apices extending beyond the ventroapical margins as convergent curving blades. Situated sagittally between the parameres is the dorso-ventrally oriented pelta, a small, narrow to somewhat broad, lens- or almond shaped sclerite with a flat or concave face. Its surface bears extremely fine setae, although these are absent (lost) in most specimens, their former presence indicated

by the remaining setal bases where the setae were once attached. The exact position of the gonopore has not been located in *Allocormodes* males, but in other genera (e.g., *Tmesibasis*) it is situated at the extreme base of the 9th sternite, ventral to the GPC, where it joins the voluminous, folded, and distensible membrane that constitutes the gonosaccus. The pulvini are moderately large, elongate, finger-like, fleshy lobes that sit lateroventrad of the GPC base and bear numerous long stiff setae.

Female terminalia (A1 Figs. 28, 30, 32–34). The female genital cavity is a long, distoventrally-oriented (in lateral view) chamber with several lateral, and a few mesal, appendages. Beginning ventrally and moving dorsally, the primary structures occur in the following order: ventrovalvae (paired), linguella (unpaired, mesally situated), interdens (on anterior face of linguella), distivalvae (paired), ectoprocts (paired). The ventrovalvae form the ventrolateral-most walls of the chamber; they are separate, but convergent, ventrally. In *Allocormodes* they each consist of a thick and rigid, but weakly sclerotized, piece of tissue that originates exteriorly and laterally and folds inwardly upon itself toward the chamber interior. Dorsally the ventrovalvae also fold in upon themselves, cupping the lateral margin of the genital chamber, being somewhat shallowly (to rather deeply) invaginated in the various species. Their surfaces bear setae of various distinctive types, which are arranged in diagnostic transverse banding patterns. The lateral walls of the genital chamber are formed by extensive, deeply infolded, and loose membrane, which also bear setae often of diagnostically variable types. The linguella (A1 Figs. 32–34) is a moderately large, fleshy appendage that originates from the floor of the genital chamber, deep between the apices of the ventrovalvae and the lateral walls of the chamber. It is often dorsally expanded or bulblike, usually membranous and rigid, but sometimes very weakly sclerotized. Its ventrosagittal surface is often produced into a broad throat that diverges dorsally and bears a dense coat of stiff curved setae of various lengths and thicknesses. The interdens (A1 Figs. 32–34) is situated on the mesal surface of the often glabrous to sparsely setose throat-like portion of the linguella, ventrad of its dorsal bulblike portion with its long and robust setae, but still sometimes hidden among rather long robust setae, and is a small, transversely-oriented, usually wedge-shaped blade. The interdens sometimes has a small ventral keel, and its margin may be entire or bilobed. Its width appears to correlate with the width of the male pelta. The roof of the gential chamber is formed by the small, separate, but very proximate clamshell-shaped distivalvae. These sit immediately ventrad of the unproduced ectoprocts. The location of the gonopore is uncertain, but is likely dorsad of the linguella within the deep, distensible, membranous tissue.

Cladistic analysis

Overview

In order to better understand evolutionary relationships among *Allocormodes* species and to infer both intrageneric cladogenetic events and associated patterns of geographic distribution, a species-level phylogenetic analysis was performed. Because insufficient material yielding high-quality DNA has been available to use in the analysis, the present study is restricted to morphological characters.

Character selection and data analysis

During the course of the comprehensive morphological survey that was performed for the descriptive portion of the larger taxonomic study, particular attention was paid to those features that were unique or appeared to be derived within *Allocormodes*, and yet that were constant among two or more species and more-or-less unambiguous in their expression. These were understood to be potentially phylogenetically informative, and were documented, described, scored, and analyzed.

Several iterations of character description and analysis were performed in a 'reciprocally illuminative' manner. Characters that proved difficult to quantify or that displayed high homoplasy (had low consistency index values) in preliminary analyses were removed. An effort was made to examine features from all major anatomical systems typically treated in Neuropterida. Ultimately, 35 characters from the head, thorax, wings, abdomen and male genitalia were included in the final analysis (see 'Characters', below).

Most coded characters had either two or three states, although a few had as many as four states, and many characters were sexually dimorphic. The matrix of cladistic characters and encoded states used in the analysis is presented in A1 Table 1.

Computational methods

Analyses were performed in TNT (Goloboff et al. 2008), using the 'New Technology' approach, with default settings for the Sectorial search, Ratchet, Tree-drift and Tree-fusing algorithms. No characters were designated as additive (although the putative plesiomorphic state was coded as 0 and derived states as 1, 2, etc.). The analysis was rerun in PAUP* (Swofford 2002) and an identical topology obtained. Bremer supports were calculated in PAUP* using TreeRot (Sorenson 1999). The consistency index (C. I.) retention index (R. I.), and other statistical measures were generated in PAUP*, as were lists of taxon synapomorphies by branch (A1 Table 2) and character state changes by character (A1 Table 3).

Outgroup selection

No larger phylogenetic analysis of any part of the Ascalaphidae has yet been published (with one exception—Henry 1978b constructed a rudimentary phylogeny of the family based on optimization of characters of eye shape, repagula development and ovariole number), and phylogenetic relationships among the genera of Haplogleniinae have not been established in the literature (although clues can be derived from existing classifications; see, for example, Tjeder 1992). The position of *Allocormodes* within the Ascalaphidae, then, has been an open question. Tjeder (1992) placed *Allocormodes* in its own tribe separate from all the other African genera but did not directly discuss phylogenetic affinity, although he did point out a few general similarities to some other genera (see next paragraph). Comparison of *Allocormodes* species to other genera of African Haplogleniinae indicates they are quite different. In particular, *Allocormodes* are much larger overall, have much shorter, stouter abdomens, and the bases of their fore- and hind wings are notably broad and unreduced. This latter feature, in particular, is notable—nearly all other genera of African Haplogleniinae have the wing bases somewhat to considerably narrowed. *Proctolyra* Tjeder is the only other entire-eyed African genus with unreduced wing bases, but a physical examination of its species suggests it does not belong within the Haplogleniinae.

Comparisons of Ascalaphidae to other myrmeleontiform families indicates that broad forewing and hind wing bases are plesiomorphic in Ascalaphidae. Thus *Allocormodes*, if united with the African Haplogleniinae fauna, may be among its most plesiomorphic genera. Examinations of other African Haplogleniinae reveal few shared apomorphies, but many potentially shared plesiomorphies. For example, *Campylophlebia* McLachlan, *Neocampylophlebia* van der Weele, and *Cormodophlebia* van der Weele are all also large-winged with stout bodies. However, their wing bases are considerably narrowed, indicating they are all more derived than *Allocormodes*, and they express few distinct similarities with the genus.

Ongoing analyses of unpublished molecular data (chapter 4) verify that the African Haplogleniinae fauna is highly cohesive (*Proctolyra* has not yet been included) and independent from Haplogleniinae in other parts of the world. They place *Allocormodes* together with the African genera *Tmesibasis* McLachlan, *Neocampylophlebia* and *Balanopteryx* Karsch. None of these genera present themselves as good candidates for outgroups, however, because they are all putatively highly-derived and display few physical similarities with *Allocormodes*. However, a clade containing a small group of genera was placed basad of the *Allocormodes* clade and includes *Melambrotus* McLachlan and *Neomelambrotus* van der Weele (two genera with very narrowed wing bases). Based on this assessment, the very similar and putatively more plesiomorphic genus *Paramelambrotus* (it has somewhat broader wing bases) was selected as an outgroup for this study and coded from Tjeder's (1992) original description and figures. In addition, *Amoea* Lefèbvre and *Albardia* van der Weele were also included. *Amoea* was selected because, like *Allocormodes*, it possesses broad wing bases, and molecular analyses indicate it sits at the base of the Haplogleniinae of the Western Hemisphere, which are monophyletic. *Albardia*, from Brazil, was selected because of its position as the sole member of the monobasic and putatively basal owlfly subfamily Albardiinae.

Characters

The following character systems, characters and states were used in this analysis (see A1 Table 1 for coded matrix). Character optimizations across the phylogeny are discussed in the results sections for each character, below (see also character state change list, A1 Table 3).

Head

[1] Average antennae length to forewing length ratio, males

0 Very short, < 0.20

1 Medium length, 0.21–0.83

2 Long, ≥ 0.83

Comments: Antennae length and forewing length were measured for each available specimen and ratios generated. Average ratios across each species were then compared (see A1Excel file 2).

Results: Very short antennae occur in the outgroup, *Albardia*. In most species of *Allocormodes* the antennae are only moderately long, but they much longer in *A. lefebvrei*.

[2] Flagellomere nodes

0 Not considerably expanded apically

1 Conspicuously expanded apically

Results: State 1 is a feature of *A. kolbei* and *A. lefebvrei*. Other species do not show this expansion.

[3] Flagellomere internodes, setitori

0 Absent, inconspicuous, or few in number on a few distal flagellomeres

1 Present, conspicuous, and dense in at least distal half of flagellum

Comments: Setitori, when expressed, are found along the full length of the flagellum, but become increasingly swollen and dense distally, and are most conspicuous near the antennal clubs. They are sometimes darkened with pigment. Species without setitori sometimes have setal spots (see Character 5, below).

Results: State 1 is strongly expressed in *A. kolbei* and slightly less so in *A. lefebvrei*. Well-developed setitori are a highly-derived feature.

[4] Flagellomere nodes in basal fourth of antennae, non-verticil setae

0 Absent

1 Present, short, length less than flagellomere diameter at apex

2 Present, long, length equal to or longer than flagellomere diameter at apex

Comments: When elongate, the setae are also slightly more robust.

Results: The presence of nodal setae is a synapomorphy for *Allocormodes*. Long setae on the flagellomere nodes are a conspicuous feature of *A. lefebvrei* and *A. kolbei*.

[5] Flagellomere internodes in basal fourth of antennae, non-verticil setae

0 Absent

1 Present, inconspicious, slender

2 Present, conspicuous, robust

Comments: Characters 3 and 4 encode identically, and the use of both in the analysis may be redundant. However, they treat different parts of the flagellomere, and the setae they address do not have the same qualities, suggesting at least some degree of functional independence. For that reason they are both retained.

Results: Robustness of setae occurring on flagellomere internodes is a feature of *A. kolbei* and *A. lefebvrei*. In the end, their mutual inclusion has no effect on the shape of the final topology, but Bremer support along the branch leading leading to *A. lefebvrei* and *A. kolbei* is increased.

[6] Flagellomere internodes in distal half of antennae, setal spots

0 Absent or very weakly developed, if present then only at the base of a few setae

1 Present at base of most setae

Comments: Setitori of some species are marked with pigment spots, but in other species there are spots without setitorus development. Thus, the maculae were coded separately from the setitori.

Results: The presence of spots is a synapomorphy for the clade containing *A. albus*, *A. lefebvrei* and *A. kolbei* (node 11—see A1 Fig. 1). They have also independently arisen in *A. junodi* and *A. maynei*.

Thorax

[7] Cervical sclerite, apex color

0 Brown (pale brown to dark brown)

1 Yellowish (dull to intense) or reddish (pale)

Comments: There is some intraspecific variation of this feature, but it occurs only rarely.

Results: Sclerite coloration is highly variable among the species. Yellow sclerites were recovered as a synapomorphy for a large group of *Allocormodes* species (node 5—see A1 Fig. 1), but the sclerites are brown in two species within the clade, *A. maynei* and *A. nigris*. Yellow sclerites are also seen in *A. albus*.

[8] Pleural setae color

0 Predominately pale orangish yellow

1 Predominantly brown

2 Predominately white or pale yellow

Comments: Setae color is fairly even across the pleuron in most species.

Results: Brown pleural setae is a synapomorphy for the largest clade within *Allocormodes* (node 4). The other large clade has pale yellowish or white pleural setae, similar to the outgroup *Paramelambrotus*, except for *A. kolbei*, which has brown pleural setae.

[9] Mesoscutal velvety spots

0 Absent

1 Present

Comments: These spots are perfectly round and black on the mesoscutum.

Results: Spots occur in the outgroup *Paramelambrotus* and in *Allocormodes*. The spots are absent in *A. albus*.

[10] Mesoscutal velvety spots size

0 Absent

1 Present, small

2 Present, large

Comments: Velvety spot size is fairly constant across the species of *Allocormodes*.

Results: In *A. maculipennis* the spots are nearly twice as large as in other species (see A1. Fig. 86).

[11] Mesothoracic notum, pale setae postolaterad of velvety spots

0 Absent

1 Present

Comments: In many *Allocormodes* the pteronotum is evenly covered in brown or white setae, but in some species there are patches of white setae amongst the primarily dark background setae, including notably behind the mesoscutal velvety spots.

Results: The patches of white setae occur in members of one clade (node 6), but are lost in *A. nigristigma*.

[12] Mesoscutellum posterior margin white setae

0 Absent

1 Present

Comments: The posterior margin of the mesoscutellum is glabrous in most *Allocormodes* species but bears pale setae in a few.

Results: The presence of white setae is a synapomorphy for the clade containing *A. nigristigma*, *A. nigris* and *A. micheli* (node 8).

[13] Mesoscutellum posterior margin white setae fringe

0 Absent

1 Present, dense, setae short

2 Present, sparse, setae moderately short

Results: The mesoscutellal posterior marginal setae are developed into a fringe of evenly short white setae in *A. micheli*.

Legs

[14] Pro- and mesothoracic femora, color

0 black

1 predominately dark brown

2 predominately pale yellowish brown

3 dorsally pale, ventrally dark

Results: Predominately dark brown femora unite five species of *Allocormodes* (node 6).

Wings

[15] Hind wing length to forewing length ratio, males

0 < 0.92

1 ≥ 0.92

Comments: See A1 Excel file 2for measurements and ratios.

Results: Nearly co-equal fore- and hind wings is an autapomorphy for *A. lefebvrei*.

[16] Pre-stigmal cells subtending R in radial space

0 Approximately as high as wide

1 Much wider than high (width often 2x height)

Results: State 1 seen in *A. maculipennis*, *A. maynei*, and *A. albus*.

[17] FW apex outline, males

0 Slightly asymmetrical, sometimes subacute

1 Symmetrically round, obtuse

Comments: In species with the highly rounded forewing tips the character is expressed only in males.

Results: Extremely symmetrical roundness of the wingtips occurs in *A. kolbei* and *A. lefebvrei*.

[18] FW apex outline, females

0 Convex

1 Anteriorly slightly emarginate

Comments: It is not certain if emargination also occurs in males as the only species expressing it was represented by a single female.

Results: State 1 was seen only in *A. albus*.

[19] FW margin distad of anal angle, outline

0 Convex to weakly concave, anal angle not produced

1 Concave, anal angle at least slightly produced

Comments: In *Allocormodes*, narrowing of the wing bases occurs in both wings and both sexes (see characters 27 and 28, below), but occurs more often in the forewings, indicating that selection pressure toward reduction is stronger in the forewings than in the hind wings. Females also tend to have narrower wings than males.

Results: State 1 is the derived condition. Forewing narrowing occurs in *A. albus*, *A. lefebvrei* and *A. kolbei* (node 11).

[20] FW Sc crossveins

0 0-2

1 5-20

Comments: The presence of these crossveins in *Allocormodes* may be unique within the Ascalaphidae.

Results: The crossveins are a synapomorphy for four species (node 10).

[21] FW pterostigmal area pigment color, males

0 Absent or evenly very pale brown

1 Present, orangish brown or orangish cream

2 Present, completely white or cream

3 Present, proximally dark brown, distally pale cream

Comments: In spite of a similarity in color, cream-colored pterostigmal pigment contrasts with that of the apical pigment patch and can be easily distinguished.

Results: Completely cream-colored FW pterostigmata are a synapomorphy of four species (node 10).

[22] FW apical pigment patch pigment, males

0 Absent

1 Present, restricted primarily to apical area and compressed marginal domain

2 Present, covering most of wingtip distad of pterostigma, but posterior portion comprising only ca. 3 cells in radial area

3 Present, covering most of wingtip distad of pterostigma, but posterior portion comprising ca. 8 cells in radial area

4 Present, covering wingtip from Mp_1

Comments: Specimens expressed some intraspecific plasticity in the square area of the pigment patch, but this variation is captured within the given states of this character.

Results: The various states of the patch are synapomorphies for several small groups. State 1 unites two species (node 9). State 2 unites five species (node 6), but is reversed at node 9. State 3 unites four species (node 10).

[23] FW pigment, maculation appearance

0 Absent

1 Present, edges of maculations soft and subdued, blending into non-pigment membrane

2 Present, edges of maculations coarse and sharp, contrasted with non-pigment membrane

Comments: Wing pigment in most *Allocormodes* species consists of margining of crossveins that evenly blends and fades out in the cell membranes.

Results: Pigment is more sharply defined in *A. maynei*.

[24] FW pigment, cubital area

0 Absent

1 Present, triplet of margined veins in cubital area

Results: The triplet of margining occurs uniquely in *A. maculipennis*.

[25] FW pigment, cells subtending R in radial area

0 Absent

1 Present, cells laterally margined

2 Present, cells completely filled with pigment

Results: Margining of cells occurs in most *Allocormodes* species but is lost in three species (node 11).

[26] HW costal area

0 Basally broad, C and Sc not parallel throughout length

1 Basally narrow, C and Sc essentially parallel throughout length

Comments: In a few species coded for state 1 the basal expansion is only slight, but in these cases the space between C and Sc also narrows slightly before the pterostigma.

Results: Evenly narrow costal areas occur in *A. lefebvrei* and *A. kolbei* (node 12).

[27] HW margin posterad of marginal cell(s), outline, males

0 Convex

1 Concave

2 Very convex to Mp_1

Comments: The states of this character were analyzed as non-additive. State 2 refers to the outgroup *Amoea*, in which males have the hind wing margin very broad from the wing base to Mp_1.

Results: Narrowing occurs in three species (node 11) and to a lesser degree in *A. micheli*.

[28] HW margin proximad of marginal cell(s), outline, females

0 Convex

1 Weakly concave, nearly straight

2 Distinctly concave

Comments: This character codes differently for males and females in *A. intractabilis*, and thus it was split (see character 27, above) to accommodate the two sexes.

Results: HW narrowing in females is a synapomorphy for *A. lefebvrei* and *A. kolbei* (node 12). The wing expands in *A. junodi*.

[29] HW medial triangle, distal domain shape

0 absent

1 elongate

2 short

Results: The domain is significantly reduced in *A. lefebvrei*.

[30] HW medial triangle, number of distal domain (post-fork) crossveins

0 2-4

1 0-1

Comments: The two states of this character code cleanly for several species, but on a specimen level exhibit some variation in other species. Surveying across many specimens for each species was necessary to determine the "average" state, which was then coded for the species.

Results: Neither of the two states of this character were optimized as synapomorphies for any included taxon.

[31] HW pterostigma pigment, color

0 Absent

1 Present, orangish cream or orangish brown

2 Present, pale whitish-cream

3 Present, proximally brown and distally cream

4 Present, completely very dark brown

Comments: There is some variation in the expression of state 3—the most common pigmentation pattern seen in *Allocormodes*—both within and among species. For example, sometimes the pigment is only weakly expressed.

Results: Very dark brown HW pterostigmata are an autapomorphy for *A. nigristigma*.

[32] HW pigment

0 Absent

1 Present, maculations linear, arranged mesolongitudinally

2 Present, maculations non-linear, arranged variously but not strictly mesolongitudinally

3 Present, margining along major longitudinal veins

Comments: Linearity of the maculation is most well-expressed in *A. intractabilis*, and most other *Allocormodes* species also have more-or-less linearly arrange blotches.

Results: Irregular blotches of pigment (state 2) occur in *A. maynei*.

[33] HW marginal cell maculation

0 Absent

1 Present, at anastomosis only

2 Present, continuing past anastomosis as margining along several crossveins

Comments: The maculation refers to a distinct brown macula positioned at convergence of Mp_{2p}, Cua, and the proximal end of the crossveins/veinlets forming the marginal cell(s).

Results: This character occurs only in *A. junodi*.

Abdomen

[34] Abdomen shape, males

0 Narrow throughout, elongate (different from females, which have broader abdomens)

1 Humped and expanded basally, narrowing apically (similar to females)

Comments: Similar abdomen shape between the sexes is a feature only seen in a few haplogleniine genera, including *Allocormodes* and *Protidricerus*, and was utilized here to separate the genus from the outgroup.

[35] Pelta, ventral margin, outline

0 Poorly differentiated from gonarcus

1 Well differentiated from gonarcus, acuminate

2 Well differentiated from gonarcus, blunt

Comments: The shape of the ventral reach of the pelta is rather conspicuous in most species, either converging to a sharp point, or being distinctly blunt.

Results: The ventral margin blunt is a synapomorphy for a clade of five species (node 5), but reverses to acuminate in one of them, *A. micheli*.

Results

Taxonomic placements and support

The analysis resulted in a single most-parsimonious tree with a completely resolved topology (A1 Fig. 1). The tree has the following statistical properties: length 79 steps; number of parsimony-informative characters: 29; consistency index (CI) = 0.7468; homoplasy index (HI) = 0.2532; CI excluding uninformative characters = 0.7183; HI excluding uninformative characters = 0.2817; retention index (RI) = 0.7015; rescaled consistency index (RC) = 0.5239.

Allocormodes was recovered as monophyletic, although with low Bremer support (node 3: 1). A single synapomorphy was recovered for the genus, the presence of nodal setae (character 4, state 1). Within the genus, the species are nearly equally split into two large clades, but with low Bremer support (node 4: 1; node 10:1). One of these (node 4) contains *A. inconspicuus* and related species and is united by dark pleural setae (character 8, state 1). The other (node 10) contains *A. intractabilis* and related species and is united by the following synapomorphies: the FW subcostal area with 5-10 subcostal crossveins (character 20, state 1), the FW pterostigmal area of males with pigment completely white or cream (character 21, state 2), and the FW apical pigment patch of males covering most of wingtip distad of pterostigma, but with the posterior portion comprising ca. 8 cells in radial area (character 22, state 3).

Within these clades support for relationships are generally low (Bremer support value: 1), with a few exceptions. The relationship among five species (node 5) including *A. maculipennis* has a support value of 2 and is supported by the following synapomorphies: pro- and mesothoracic femora predominately dark brown (character 14, state 1); and the FW apical pigment patch of males covering most of wingtip distad of pterostigma, but with the posterior portion comprising only ca. 3 cells in radial area (character 22, state 2). And *A. kolbei* and *A. lefebvrei* are very well supported as sister taxa (node 12: 6). The following synapomorphies unite them: flagellomere nodes conspicuously expanded apically (character 2, state 1); flagellomere internode setitori conspicuous and dense in at least distal half of flagellum (character 3, state 1); flagellomere node non-verticil setae in basal fourth of antennae long, length equal to or longer than flagellomere diameter at apex (character 4, state 2); flagellomere internode non-verticil setae in basal fourth of antennae conspicuous, robust (character 5, state 2); FW cells subtending R in radial area laterally margined (character 25, state 1); HW costal area basally narrow, with C and Sc essentially parallel throughout length (character 26, state 1); and the outline of the HW margin proximad of marginal cell(s) in females distinctly concave (character 28, state 2).

The larger clade containing *A. inconspicuus* and related species does not present obvious unidirectional trends in character evolution across all its taxa. However, the various clades within it are united by several synapomorphies. *Allocormodes nigris* and *A. micheli* (node 9) are united by the FW apical pigment patch pigment in males being restricted primarily to apical area and compressed marginal domain (character 22, state 1). They are united with *A. nigristigma* (node 8) by the following synapomorphies: mesoscutellum posterior margin with white setae (character 23, state 1); and these moderately short (character 13, state 2). *Allocormodes maculipennis* and *A. maynei* share enlarged pre-stigmal cells subtending R in the radial space (character 16, state 1). Some similarities are also seen in the basally placed species: *A. inconspicuus* and *A. junodi* both lack white pigment on the membrane in the area of the apical pigment patch.

However, this latter feature was not placed as a synapomorphy for them and instead appears to be plesiomorphic within the clade.

The other large clade containing *A. intractabilis* and related species does seem to display more distinct unidirectional trends. The following general observations can be made (some of these are synapomorphies at various levels within the clade): lengthening of the antennae (character 1); an increase in the robustness of the antennae, as expressed by a slight expansion of the distal margins of the flagellomeres (character 2); lengthening and thickening of nodal and intermodal setae (characters 4, 5); an increase in the size and density of the setitori (character 3); lengthening of the hind wings (character 15); narrowing of the wing bases (characters 19, 27, 28); the appearance and increase in number of the subcostal crossveins (character 20); and an increased density in the cells of the compressed marginal domain (not coded).

Taxonomic treatments

Format

The following general format is used herein for taxon descriptions:

Name. The current, valid taxon name is used as a header, followed by any new taxonomic actions taken here, e.g., “n. sp”, “n. subsp.”

Type species. The type species epithet is provided in italics.

Taxonomic history. Works critical to the taxonomic and nomenclatural development of a taxon (e.g., original descriptions, redescriptions, keys, erections of replacement names, discussions of evolutionary/natural relationships, etc.) are given in chronological order. Following the author names the year of publication is given, proceeded by, if pertinent for nomenclatural purposes, the exact date of publication in the following format: year.month.day. Reference numbers used in the Bibliography of the Neuropterida (Oswald 2013) are provided (in the format r#00000) to allow for quick referencing to comprehensive bibliographic information and, for many references, downloaded PDF copies, presented therein. Notes on taxonomic and nomenclatural content of cited works are given in curly brackets {}. In cases of misidentification, taxon names in synonymical lists are bounded by square brackets [].

Etymology and nomenclatural notes. Language origin is provided for each putative root component of the taxon epithet, as well as additional notes concerning name selection by the describing author. Gender, for genus, is provided for nomenclatural purposes. Species epithets are indicated as 'noun in apposition' or 'adjectival', when applicable. Direct quotes from source literature are placed in double quotes ("") and translations in single quotes ('').

Diagnosis. A brief diagnosis is given of the features that set apart a particular taxon from other closely related taxa within the containing group (e.g., other species within the genus). This may include suites of plesiomorphies, synapomorphies, or both.

Proposed synapomorphies/autapomorphies. This list is extracted from results determined in the cladistic analysis. See also A1 Table 2 for a list of synapomorphies.

Descriptions. A comprehensive description of the external anatomy and terminalia of each putative taxon is presented, based on examination of all available specimens.

Size. Measurements were made using a Tresna Instruments plane, parallax-free, 0.02 mm accurate vernier caliper, and are rounded off to the nearest millimeter. For species in which multiple specimens were measured, minimum, average and maximum length measurements are given in the format: avg (min–max), e.g., 30 (27–32). Many examined specimens were broken and lacked antennae, abdomens, wings, etc. In order to maximize measurement sample sizes, available features were measured even if other features were missing on the same specimen. Measurements made for each specimen (using the JRJ database number) are available in A1 Excel file 2.

Variation. Within each species are specimens that express one of more features in a variable or anomalous manner; the type and degree of variation in these specimens is presented, along with their database number for later consultation. This should maximally enable later corroboration (or restructuring, where necessary) of the taxonomic concepts worked out herein.

Natural history and immature stages. The information presented here has been derived from the literature, label data, and the specimens themselves. The data include adult flight period, circadian activity (as indicated by attractions to collecting lights or other label and literature notes), habitat data, plant associations, larval biology, and other facts as known.

Distribution. A summary phrase describing known range is given, followed by a list of specific countries in which the species has been confirmed to occur, based on label data of examined specimens and literature that can be unambiguously interpreted under the new taxon concepts presented in this work. Distribution maps with plots of the localities of examined specimens (and those positively confirmed from the literature) are provided for each species. Country lists are based on political entities current as of January 2013. The latitude and longitude coordinates of collection localities have been extracted (when explicitly designated) or estimated (when not explicitly designated) from specimen labels or the literature, and are given in the A1 Excel file 1.

Type material examined. A list of specimens examined for this project and either designated newly in this revision or by past researchers as name-bearing types (holotypes, lectotypes, syntypes, neotypes) is provided for both taxonomic and nomenclatural purposes. These determinations are explained in an included notes section. For each specimen listed, label data is written verbatim, and individual labels are separated from one another in the sequence in which they occur on pins by three forward slashes ' /// '. The condition of the specimen at the time of examination is also provided. Specimens having been designated by past researchers in non-name-bearing roles (e.g., paratypes, allotypes, etc.) are included under 'Additional material examined, (see below).

Additional material examined. Specimens are listed alphabetically by coden (see coden list under 'Material', above), then country, then gender, beginning with males, and include country of origin and a JRJ database number (see 'Databasing' above). Countries are recorded here using their current names, with the name given on the label provided parenthetically and in quotes ("") where there is a discrepancy.

Discussion. Any information regarding the taxon not included in any previous section is presented here.

Genus **Allocormodes** ***McLachlan, 1891***

Type species *Ascalaphus intractabilis* Walker, 1860

Cormodes McLachlan, 1871

—McLachlan 1871.09.14 r#353: 239 {TSP: *Ascalaphus intractabilis* Walker. TS: not explicitly indicated [holotype by explicit monotypy]. GD, OD, K.}

Allocormodes McLachlan, 1891

—McLachlan 1891 r#385: 512 {TSP: *Ascalaphus intractabilis* Walker. TS: not explicitly indicated [holotype by monotypy in *Cormodes* McLachlan]. NN ("*Allocormodes*" as objective replacement name for *Cormodes* Pascoe, 1861, preoccupied by *Cormodes* Pascoe, 1861—see Oswald and Penny, 1991).}

—Kolbe 1897 r#3434: 26 {K, RD}

—van der Weele 1909.01.05 r#420: 71 {DIS, GD, IS, K, MON, RD, SYN, TSP}

—Tjeder 1992 r#7246: 165 {TGEN (of new tribe Allocormodini)}

Etymology and nomenclatural notes.—*Allocormodes*: allos (Greek), 'other' + kormos (Greek) 'trunk of a tree' + -odes (Greek) 'like or resembling', = 'resembling a tree trunk'. *Gender*: masculine. Virtually nothing was published on the biology of members of this genus prior to McLachlan's creation of the genus, and he provided no information regarding his name selection in his revision (1871) or subsequent new name designation (1891); but the name seems aptly applied, as evidence presented herein suggests a strong affinity of both larvae and adults of the species to trees: the larvae on bark, the adults in foliage.

Diagnosis.—Large owlflies (FW 30–48 mm). Wings: anterior and posterior margins essentially parallel in distal two thirds; apices broad, usually more-or-less symmetrically rounded; FW anal angle generally unproduced, slightly produced and subacute in a few species, and both wing bases slightly narrowed in these same species; pigment margining bordering at least some, but usually many, veinlets and crossveins, often arranged in a long, narrow, broken, mesal band following the long axis of both wings; male FW apex usually with a patch of white pigment, but in some species indicated only as an area of pale veins; male wings of a few species often melanistic. Abdomen: short, ca. half FW wing length, more-or-less stout; terga of males without projections; ectoprocts of males and females simple, unproduced.

Proposed synapomorphies.—Flagellomere nodes in basal fourth of antennae with non-verticil setae short, length less than flagellomere diameter at apex.

Description.—

Size (mm). Male: body length 23-37, abdomen 11-20, forewing 30-45, hind wing 26-41, antennae 20-38. Female: body length 22-32, abdomen 12-22, forewing 33-48, hind wing 28-43, antennae 21-36.

Head. (A1 Figs. 2–15). Width at eyes as wide or wider than thorax at base of mesothoracic wings. Occiput glabrous, glossy, color varying from dull yellow to dark reddish brown, sometimes with irregular yellowish maculae, these occasionally plate-like. Postorbital sclerite very narrow, glabrous, color variously pinkish to yellowish brown to dark brown, often concolorous with occiput. Vertex swollen dorsally; epicranial suture more-or-less distinct, vertex bilobed. Vertex pattern slightly asymmetrical from side to side, lateral plates variable in shape, dull orangish brown to bright yellow, usually conspicuous and slightly raised, but sometimes weakly distinguishable from dark regions, dark regions bearing a silvery microtrichiaand a sparse to dense coat of long very slenderwhite, yellow or brown setae. Anterior extra-torular sclerites pale to bright yellow, occasionally amber- or dark reddish brown and concolorous with frons, fused but deeply invaginated medially. Frons yellowish to pale or dark reddish brown, swollen, bearing moderately dense covering of long brown to dark brown very slendersetae. Clypeus broad, swollen, surface shallowly grooved transversely, narrowing ventrally to labrum, pale or dull yellow or amber to dark reddish brown, bearing long brown to dark brown curving setae, these denser and thicker laterally. Paraocular band narrow, color variable, often darker near antennae and paler near clypeus and mandible bases, portion adjacent to clypeus and lower part of frons bearing a patch of somewhat laterally appressed medium length thin dark brown setae. Anterior tentorial pit a dorso-ventral slit, usually closed but sometimes open, particularly ventrally as a small pore. Pleurostoma absent. Posterior genal triangle narrow, glabrous, dull yellowish to dark reddish brown. *Mouthparts.* Labrum glossy, amber to dark reddish brown, lateral and ventral margins with medium- to long, stiff, golden and/or dark brown, slightly ventrally-curving setae. Mandibles essentially brown, usually dull or orangish brown basally, reddish brown subapically, apices dark brown, bearing medium length thin dark brown to black setae. Maxillary stipes and palpomeres yellow or dull amber to dark reddish brown, stipes and palpomere 1 with long brown to dark brown setae, palpomeres with apical whorls of short stiff black setae. Labium: submentum and mentum yellow or dull amber to dark reddish brown, with long dull yellow to dark brown setae; labial palpi 3-segmented, dull amber to reddish brown, palpomeres bearing numerous short stiff black setae; ligula dull yellow to amber to granularly reddish brown, rarely with a faint narrow median longitudinal dark brown stripe, ventrally glabrous, apico-dorsally with short recurved golden brown setae. *Eyes*. Golden to dark reddish brown. *Antennae.* Scape shorter than wide, globose, yellowish to reddish or dark brown, bearing a dense coat of very long brown to dark brown setae. Pedicel length less than half width, orange to dark reddish brown, distal margin often a pale orange or red ring. Flagellum with 26–32 flagellomeres, color variable but usually yellowish to dark brown, flagellomeres often paler and nodes darker with a pale distal margin, basal flagellomere with a few long slender ventrolateral verticils, verticils absent on dorsal surfaces, all flagellomeres bearing short black setae, setitori absent to well developed.

Club with six to fourteen flagellomeres, elongate ovoid, apical segment blunt, often with a minute apical acumination; color variable, from completely pale yellowish to dark brown, often darker dorsally and paler ventrally, sometimes appearing dark due to abundance of dark reddish brown maculae at bases of setae; setae numerous, short, black.

Thorax (A1 Figs. 16–18). *Cervix*. Dorsal cervical plates yellow or orange to dark brown, with variable color patterns, bearing long very slenderwhite and/or brown to dark brown setae. Cervical sclerite yellow or dull orange to pale or dark brown, apical surface covered with pale appressed microtrichia, anterior surfaces bearing numerous long very slenderbrown to dark brown setae. Ventral cervical plate knob-like, elongate to ovoid, yellow to dark brown, bearing very long very slenderbrown setae. *Pronotum*. Short, with somewhat numerous, long, wispy, pale to dark brown and sometimes white setae. Prescutum very narrow longitudinally but prominent, raised dorsally, divided medially, usually rather weakly, by a longitudinal sulcus, thus appearing bilobed, pattern of yellow and brown variable. Scutum narrow longitudinally, median sulcus obscure or absent, depressed and undeveloped dorsally, usually with a small circular median depression, pattern of yellow and brown variable, posterolateral knob reddish to dark brown, bearing numerous, long, dark, very slendersetae. Scutellum narrow longitudinally, raised dorsally but not produced into a flange posteriorly, weakly divided medially by longitudinal sulcus, pattern of yellow and brown variable, setae numerous, long, wispy, usually brown, but sometimes also white or yellow. *Mesonotum*. Large, highly domed, elevated above prothorax, wing bases and metathorax. Prescutum cordiform, distinctly divided into two lobes by sagittal sulcus/depression, posterior margin bordering scutum a thin distinct sulcus, color brown with variable yellow or orange patterning, setae long, wispy, brown and sometimes white. Scutum weakly divided by thin sagittal sulcus, expanding laterally to form large round lobes, brown to dark brown, with highly variable patterning of yellow to orange; setae variable, usually brown, but often with diagnostic white or yellow patches, tegular setae undifferentiated from other setae; velvety spots distinct, round, very dark brown, situated anteromedially on each lobe. Scutellum swollen, dorsal elevation highest of thorax, not bilobed, sagittal sulcus evident but thin and weakly expressed, posterior margin transversely swollen, overall color brown to dark brown, with highly variable patterning of yellow to orange, setae brown, yellow and/or white, color and distribution often diagnostic. Subscutellum a thin undeveloped flange, color variably brown, yellow and/or orange. Postnotum somewhat narrow longitudinally, transversely broad, bilobed, yellowish to dark brown, glabrous, often obscured under setae of scutellum. *Metanotum*. Paraprescutum brown and/or yellow, glabrous, obscured by posterior fringe of white setae of metascutellum and forewing axillary cord. Prescutum color patterns highly variable, usually glabrous but occasionally with sparse very slendersetae. Scutum obliterate medially, present as large lateral lobes, velvety spots absent, but cinnamon to dark brown microtrichia to receive FW axillary angles present, color pattern variable, setae brown, white and/or yellow. Scutellum round, domed, not bilobed, with posterior margin swollen transversely, color pattern of brown and orange or yellow highly variable, setae long, wispy, white and/or brown. *Pleuron*. Large, pleurites usually evenly brown but sometimes with yellowish maculations, setae in a sparse to thick coat, long, wispy, usually brown but sometimes white or golden yellow.

Legs (A1 Figs. 19–21). Coxae brown, with a thick coat of long very slendersetae, usually pale to dark brown but sometimes white or dull yellowish. Femora and tibiae (which lack microtrichia) with true colors and patterns often obscured by age of specimens, but likely deep reddish brown and yellow; in mounted specimens, dark reddish brown to dull yellowish, when paler, often with reddish brown spots at base of all stiff dark setae, color often different from somite to somite; setae as follows: *prothoracic leg setae*: FD: long stiff black, in some species long very slenderwhite; FV: short slender stiff black; FAL: short slender stiff black, some white in one species; FPL: long stiff black, in a few species mixed with long very slenderwhite; TD: medium long stiff black; TV: short to medium long stiff black; TAL: preening patch golden yellow, except for a few setae black proximally and/or distally; TPL: long thin stiff black; *mesothoracic leg setae*: FD: highly variable among species: short to long, stiff to slender black and/or slender white; FV: highly variable among species: short to long, stiff to slender, black or brown, and/or slender long white or long slender dull yellow; FAL: highly variable among species: short to long, stiff to very slender, black, and/or medium to long, dull yellow or brown; FPL: long stiff black, in some species mixed with long and slender white, dull yellow or brown; TD: medium long stiff slender black sometimes mixed with short slender black, sometimes only present distally or glabrous mesolongitudinally; TV: medium to very long stiff black, sometimes mixed with short slender black, longer setae often arranged in slightly laterally directed rows to avoid striking ventral surface of occluding femur; TAL: short to medium long stiff black, sometimes mixed with longer slender black; TPL: short to medium long stiff black, sometimes mixed with longer slender black; *metathoracic leg setae*: FD: highly variable among species: very short to long stiff black, and/or long slender black or very short stiff white or long very slenderwhite; FV: highly variable among species: short and slender to long stiff black and/or long dull yellowish or very slenderwhite; FAL: highly variable among species: short and slender to long stiff black and/or long dull yellowish or very slenderwhite; FPL: highly variable among species: short and slender to long stiff black, and/or long dull yellowish or very slenderwhite; TD: short and/or medium long stiff slender black, sometimes glabrous mesolongitudinally; TV: short and/or medium to long stiff slender black, sometimes glabrous mesolongitudinally, often arranged in slightly laterally directed rows to avoid striking ventral surface of occluding femur; TAL: short and/or medium to long stiff slender black; TPL: short and/or medium to long stiff slender black. Tibial spurs varying slightly in length and curvature, sometimes between males and females (but inconsistently so), as long as first three or four tarsomeres together, deep reddish brown. *Tarsi*. First four tarsomeres short, coequal in length, collective length slightly shorter than to equal that of apical tarsomere; usually reddish brown, sometimes yellowish or orangish; setae numerous, short, curved, stiff, black, ventrally particularly robust and more-or-less in two longitudinal rows. Claws robust, approximately two-thirds length of apical tarsomere, deep reddish brown.

Wings (A1 Figs. 22–26). Anterior and posterior margins essentially parallel in distal two thirds, apices broad, usually more-or-less symmetrically rounded, more symmetrical in FW; wings similar in shape, but HW slightly shorter and narrower than FW; wings usually slightly larger and with apices slightly subacute in males, in females more symmetrical. Veins, veinlets and crossveins dorsally with sparse, very short, stiff, curved, black setae, ventrally bearing more numerous medium short stiff black setae; costa with anterior margin densely lined with four rows of minute, appressed, stiff black setae, reduced to two rows along posterior margin, ventral row with many more setae; color of setae along the ambient vein and axillary cord varied. Cell membranes glabrous, glossy, hyaline; males of a few species—'melanistics'—exhibit considerable darkening of membranes. Major longitudinal and many crossveins usually reddish to dark brown, sometimes partly or completely yellow; veinlets and crossveins reddish to dark brown and yellow, often brown ventrally. Costal area either not wider in basal part of wing and essentially parallel from near base to pterostigma, or wider anteriorly in proximal one-fifth to one-third of wing, then gradually narrowing to become more-or-less parallel until proximad of pterostigma, and then expanding again slightly around pterostigma. Subcostal veinlets essentially perpendicular to Sc, sometimes slightly inclined toward wing apex, except at extreme base of wing where they incline slightly toward wing base. Pterostigma pigment spanning four to eight simple and/or branched subcostal veinlets, color opaque cream or yellow, often partially to completely suffused with granularly reddish to dark brown pigment, pigment sometimes absent, sometimes differing between fore- and hind wing, color often diagnostic. Apical area containing three to ten simple and/or branched subcostal veinlets, these joined by seven to twenty-five short, often irregularly placed crossveins. Sc space crossveins absent in most species, three to seventeen in distal half in a few species. Rs anterior trace with two to three unambiguous forks, subsequent forks often difficult to distinguish from veinlets and/or crossveins. Compressed marginal domain various both intra- and interspecifically (sometimes between left and right, fore- and hind wings), with one to four cell rows strongly narrowed and zero to two bounding rows somewhat narrowed with cells reduced. *Forewing*. Crossveins subtending R usually spaced more-or-less equally, the cells they bound approximately square, but in a few species spaced further apart, with cells distinctly rectangular. Four to eight presectoral crossveins, cells occasionally divided by irregular secondary crossveins. Four to seven prefork crossveins in cubital triangle; distal domain of triangle with one to five, often irregular, cells. One (sometimes two) marginal cells, these sometimes connected to cubital triangle by a short crossvein. Cup+1A anastomosis occurring near midpoint from origin to near point posterad of cubital fork, Cup-1A space rarely divided by crossveins. 2A arched posterad shortly after origin to fuse with 3A close to wing base, then appearing to diverge again, often anterad to join 1A and/or distad to branch into short veinlets inside anal area. 3A short, after divergence from 2A arched posteriorly to strike posterior margin of wing, or branching into short veinlets to fill part of anal area. Anal area usually with several irregular veinlets and crossveins connecting Cup+1A, 2A and 3A. Anal angle not produced, or, in a few species, slightly produced and subacute, in these species both wing bases also slightly narrowed. Posterior wing margin usually convex from anal angle to distal margin of cubital area, somewhat concave in the few species in which the anal angle is somewhat developed. *FW Maculation*. Conspicuous membrane pigment margining on some veins and crossveins, usually at least arranged in a long narrow broken mesal band following the long axis of the wing, but more extensive in some species; patterns variable among species but conserved within species and between sexes; apical pigment patch present in most species, pigment absent and veins white in two species, somewhat variably expressed within species but more-or-less consistent in size and shape among species. *Hind wing*. Two to seven presectoral crossveins. Medial triangle longer and narrower in males, with more distal domain cells, shorter and broader in females, with fewer distal domain cells; medial triangle with four to nine prefork crossveins, distal domain comprising one to six regular cells, those near fork area occasionally comprising two or more smaller cells bounded by irregular crossveins. One to four narrowly trapezoidal or triangular marginal cells. Cup+1A more-or-less straight, more-or-less paralleling Cua until reaching posterior wing margin, precise terminus often uncertain. Posterior margin usually continuously convex from wing base to base of posterior medial area, somewhat concave from anal angle to baseof posterior medial area in the few species in which the FW anal angle is somewhat developed. Maculation usually similar to that of forewing, but pigmented band often only expressed in distal half of wing, in some species extensive membrane pigment margining of veins and crossveins present in other parts of wing.

Abdomen (A1 Figs. 27–34). Outlines of T2+T3 and S3 diverging distad in lateral view; outlines of T4 and S4 sometimes parallel, sometimes converging; outlines of T5–T6 and S5–S6 converging; outlines of T7–T8 and S7–S8 converging or parallel, sometimes slightly diverging (outlines sometimes distorted in individuals with distended abdomens, as in female in A1Fig. 28); overall appearance is that abdomen is expanded dorsally. Overall color essentially brown, but variously pale to dark brown, often with distal margins of sternites and sometimes tergites contrastingly paler or yellowed, portions of T1–T3 and/or S1–S3 often paler or reddish brown to yellow. Chaetotaxy varied and often diagnostic, especially on segments 1–3, which often bear patches of dark brown and/or white and sometimes yellow setae on tergites, sternites and pleural membranes; all tergites and sternites bearing a very sparse covering of very short stiff black setae curving apicad, more dense on sternites than tergites. Ectoprocts very small, semi-circular, simple, unproduced, brown to dark brown, sometimes with yellow or orange marking; all surfaces, but especially apically bearing numerous stiff medium long black or brown (sometimes golden brown) setae. *Sexually dimorphic characteristics (non-terminalia)*. *Males*: 9th sternite posterior margin usually quadrate (or truncate), but slightly projecting medially in a few species. Pulvini sometimes protruding externally and visible in region of T9, ectoprocts and S9, finger-like, apices yellow to brown, bearing long dark setae. *Females.* Spiracle positioned laterally on T8. T9 large, ovoid to subtriangular, plate-like, dark brown, often with diffuse yellow or orange markings.

Male terminalia (A1 Figs. 27, 29, 31). Dorsal surface of gonarcus weakly to distinctly arched in lateral view, arch commencing subapically in a few species. Parameres variously sclerotized, more-or-less broad basally, apicoventral margins slightly to distinctly projecting ventrad of paramere base, often recurved in lateral view, in distal view proximate and nearly parallel to widely splayed. Pelta narrowly to broadly almond-shaped, often mesally depressed, ventral margin truncate or acuminate. Pulvini usually widely separated but sometimes proximate, somewhat broad to rather slender, length half to four times width at base, setae various, mesal surfaces often glabrous. Gonosaccal membrane between pulvini with various chaetotaxy. Hypandrium internum sclerotization various, even within species, often difficult to see.

Female terminalia (A1 Figs. 28, 30, 32–34). Distivalvae small to medium-sized, swollen semicircular to globose in outline, sometimes distinctly separated but often quite proximate, chaetotaxy various. Setae on membrane laterad of para-linguellar fold various. Linguella medium-small to large (similar in size to ventrovalvae), shape somewhat amorphous and variable, often with a ventral sagittal ridge, setae variable, often long and thick. Interdens flat, more-or-less tab-shaped, very small to moderately large. Ventrovalvae of various sizes, dorsal invagination shallow to deep, chaetotaxy various, sometimes diagnostic.

Distribution.—Africa: sub-Saharan and eastern continental tropical belts south to northeastern South Africa.

Included species.—*albus* n. sp.; *inconspicuus* n. sp.; *intractabilis* Walker; *junodi* van der Weele; *kolbei* van der Weele; *lefebvrei* van der Weele; *maculipennis* Taschenberg; *maynei* Navás; *micheli* n. sp.; *nigris* n. sp.; *nigristigma* n. sp.

Key to the species of **Allocormodes**

(adult males and females)

1. HW costal area slightly to conspicuously expanded basally, narrowing at least slightly at mid length, costa and subcosta not parallel throughout (e.g., A1 Figs. 22, 111); flagellomeres with setitori absent, or present only in few flagellomeres proximad of club, or very poorly developed 2

1’. HW costal area not expanded basally, width even throughout length to pterostigma, costa and subcosta parallel thoughout (A1 Figs. 23, 65); flagellomeres with setitori well-developed in distal half of flagellum (A1 Fig. 15) 9

2(1). Posterolateral surfaces of nota and pleura of pterothorax and dorsolateral surfaces of abdominal segments 1–3 bearing a dense coat of long, white or very pale gray setae; wing maculations arranged linearly [sub-Saharan tropical belt] .... ***intractabilis* Walker**

2’. Posterolateral surfaces of nota and pleura of pterothorax and dorsolateral surfaces of abdominal segments 1–3 with setae variable but predominantly brown, some species with isolated patches of white setae; wing maculations arranged linearly or not 3

3(2’). Cervical sclerite with apical knob bright yellow, occasionally pale brownish yellow, or with a reddish tint 4

3’. Cervical sclerite with apical knob dull to dark brown, sometimes when dark brown also with a very slight reddish tint, but never with a yellowish tint 7

4(3). Mesoscutum with pale setae posterad of velvety spot (e.g, A1 Fig. 86) 5

4’. Mesoscutum without pale setae posterad of velvety spot, all setae brown 6

5(4). FW length: male 37–38 mm, female 40–43 mm; FW often with a conspicuous ‘3’ or ‘E’ shaped maculation in basal third of cubital area near wing margin (A1 Fig. 85) [sub-Saharan tropical belt] .... ***maculipennis* Taschenberg**

5’. FW length: male 29-32 mm, female 31-35 mm; FW without conspicuous ‘3’ or ‘E’ shaped maculation [West Africa: Burkina Faso, Mali, Nigeria] .... ***micheli* n. sp.**

6(4’). HW with a small but distinct macula at apex of medial triangle (A1 Fig. 58); HW pterostigma bicolored, brown and cream, brown portion proximal and narrow [southeastern Africa] .... ***junodi* van der Weele**

6’. HW without a macula at apex of medial triangle; HW pterostigma almost completely brown, distinctly elongate and often dark [sub-Saharan tropical belt] .... ***nigristigma* n. sp.**

7(3’). FW crossveins subtending R widely spaced, most cells >1.5x as wide as high (A1 Fig. 94a); wing pigmentation aggregated into distinct non-linear maculae (A1 Fig. 92) [Democratic Republic of the Congo] .... ***maynei* Navás**

7’. FW crossveins subtending R unevenly spaced, few, if any, cells >1.5x as wide as high; wing pigmentation various but not aggregated into non-linear maculae 8

8(7’). Pterostigma weakly pigmented (translucent or pale); male apical pigment patch devoid of pigment (A1 Fig. 42); axillary setae pale grey to white [Burundi, Democratic Republic of the Congo] .... ***inconspicuus*** **n. sp.**

8’. Pterostigma strongly and opaquely pigmented (cream and/or dark brown); male apical pigment patch white (A1 Fig. 108); axillary setae very dark gray to brown [Central African Republic, Congo, Guinea] .... ***nigris*** **n. sp.**

9(1’). Distal domain of HW medial triangle short, usually containing a single cell (A1 Fig. 23); HW conspicuously narrow distad of anal angle [Cameroon, Equatorial Guinea, Uganda] .... ***lefebvrei*** **van der Weele**

9’. Distal domain of medial triangle longer, containing 2 or more cells (e.g., A1 Fig. 35); HW not, or inconspicuously, narrowed distad of anal angle 10

10(9). Mesoscutum without velvety spots (A1 Fig. 36); HW axillary sclerite setae dark brown; wing maculations very pale and weakly expressed [Angola] .... ***albus*** **n. sp.**

10’. Mesoscutum with velvety spots (A1 Fig. 69); HW axillary sclerite setae pale gray to white; wing maculation well-expressed, some males melanistic (A1 Figs. 66, 68) [Democratic Republic of the Congo, Kenya, Malawi, Tanzania] .... ***kolbei*** **van der Weele**

Allocormodes albus *n. sp.*

(A1 Figs. 35–38, 119)

Etymology and nomenclatural notes.—from *albus* (Latin), 'white'; adjectival. This species is named for the pale or whitish appearance of the type specimen, which is attributable to the weakly expressed wing maculation, cream-colored pterostigmata, white body setae, and highly reflective microtrichia on the tergum of the abdomen.

Diagnosis.—Thorax covered with dense white setae; mesoscutum without velvety spots; FW anal angle weakly produced, wing distad of angle narrowed, posterior wing margin broadly concave until proximal third of cubital area; hind wings only weakly narrowed basally; distal domains of cubital and medial triangles long, apex of cubital triangle acuminate; FW pterostigma cream colored.

Proposed autapomorphies.—cervical sclerite apex color yellow; mesoscutal velvety spots absent; pre-stigmal cells subtending R in radial space much wider than high (width often 2x height); FW apex outline of females anteriorly slightly emarginate.

Distribution (A1 Fig. 119).—Angola.

Description.—

Size (mm). Male: unknown. Female: body length 32, abdomen 19, forewing 43, hind wing 40, antennae 29.

Head. Occiput dark reddish brown. Postorbital sclerite dull pale yellow. Vertex pattern with lateral plates asymmetrical and their margins irregular, all plates orangish brown with dark brown speckling, dark regions bearing dense coat of white microtrichia and long, very slender, pale yellow setae. Anterior extra-torular sclerites very pale yellow, each slerite slightly darker mesally. Frons dark brown, setae very pale yellow. Clypeus dark brown, yellow along surfaces above transverse grooves, lateral and dorsal margins pale yellow, setae very pale yellow. Paraocular band diffusely pale dull yellow near mandible bases and along eye margin, otherwise dark brown. Anterior tentorial pit closed. Posterior genal triangle obliterate by dull pale yellow orbital sclerite. *Mouthparts.* Labrum brown, setae dark brown. Mandibles dull brown basally, dark reddish brown in apical two thirds. Maxillary stipes dull yellow, palpomeres orangish brown, stipes setae white and palpomere setae dark brown. Labium: submentum and mentum setae white and dark brown; labial palpi orangish brown; ligula dull pale yellow to amber. *Eyes.* Golden brown. *Antennae.* Scape dark brown, setae mixed dark brown and very pale yellow. Pedicel brown with orange distal margin. Flagellum with 29–30 flagellomeres, base color pale orangish brown, anterior surfaces predominantly pale but dark brown subapically, posteror surfaces predominantly dark brown but flagellomere bases and node margins thinly pale; setitori small, dark brown, becoming darker and more numerous distally toward club. Club with 12–13 flagellomeres, dark brown posteriorly, pale orangish brown anteriorly.

Thorax (A1 Fig. 36). *Cervix*. Dorsal cervical plates dorsally dark brown, otherwise pale dull yellow, setae very pale yellow. Cervical sclerite dull pale yellow, anterior subapical setae white. Ventral cervical plate knob very pale yellow, setae mostly dark brown with some very pale yellow. *Pronotum*. Setae somewhat numerous, long, wispy, mostly dark brown dorsally, laterally very pale yellow. Prescutum pale yellow, dorsally with sublateral pale black maculation. Scutum mediodorsally pale black, sublaterally and along posterior margin pale yellow, posterolateral knob pale black. Scutellum pale black dorsally but divided mesally by a narrow pale yellow stripe, pale yellow laterally. *Mesonotum*. Prescutum lobes pale yellow with numerous tiny dark flecks, pale black anteriorly and posteriorly, pale orange mesally, prescutum surface bearing long, very slender, dark brown setae dorsally, long, very slender, pale white setae laterally. Scutum color pattern diffuse, irregular, overall pale dark brown, pale yellow sublaterally along anterior margin and laterally above wing bases, diffusely pale yellow in area of velvety spots, velvety spots absent; dorsal setae sparse, very slender, dark brown, lateral setae thick, long, white. Scutellum dull dark brown, anterior swelling posteriorly with sublateral diffuse orangish maculae, posterior swelling anteriorly dark brown, divided mesally by a large orangish brown macula, posteriorly orangish brown, lateral and posterior surfaces bearing long thick white setae. Subscutellum pale yellow. Postnotum very pale dark brown. *Metanotum*. Paraprescutum yellow, very dark brown along anterior margin, glabrous. Prescutum yellow, posterior margin thinly very dark brown, glabrous. Scutum dark brown, a small yellow maculae laterally, microtrichia dark brown, lateroposterior margins bearing long thick white setae. Scutellum yellow with a broad dark brown sagittal stripe ending at posterior swelling, anterior surface of swelling bearing a narrow sublateral transverse brown stripe, posterior surfaces bearing long, very slender, white setae. *Pleuron*. Pleurites mostly dark brown, but some with pale yellow margins, and some completely pale yellow; all pleural surfaces bearing a thick coat of long, white setae.

Legs. Coxal setae long, thick, white. Femora and tibiae very pale yellowish brown, tibia dorsodistal margins glossy brown, dark brown spots on integument at bases of many setae, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long, very slender, white; FV: short slender stiff black; FAL: short slender stiff black; FPL: long, stiff black; TD: short stiff black; TV: medium length stiff black; TAL: preening patch setae orange; TPL: long thin stiff black; *mesothoracic leg setae*: FD: long, very slender, white; FV: some long stiff black proximally; FAL: long slender white; FPL: long stiff black mixed with long slender white; TD: mixed short and medium long stiff slender black; TV: mixed short and medium long slender black; TAL: short stiff slender black; TPL: mixed short and long stiff slender black; *metathoracic leg setae*: FD: long, very slender, white; FV: long stiff black; FAL: some long, very slender, white; FPL: long stiff black mixed with long slender white; TD: short slender black and one or two medium long stiff black; TV: short stiff black; TAL: short slender black; TPL: mixed short and medium long stiff slender black. Tarsus very pale yellowish brown.

Wings (A1 Fig. 35). FW apex commencing at pterostigma and continuing to half of apical area slightly concave, HW apex round. Venation very pale yellow with black margins, or black, Sc+R and compressed domain veinlets and crossveins very pale yellow. Rs with two or three clear forks. Ambient vein and axillary cord setae mixed brown and white in FW, brown in HW. *Forewing*. Costal area not expanded in basal part of wing, essentially parallel from near base to pterostigma, most costal cells wider than tall. Pterostigma comprising four or five veinlets, opaque membrane pigment occupying mesal portions of four or five cells, pale cream. Apical area containing four branched and unbranched veinlets, with five to seven crossveins. Sc space with nine crossveins in distal half. Seven presectoral crossveins. Cubital triangle with five prefork crossveins; distal domain elongate, comprising two cells, apical cell distally acuminate. One triangular marginal cell present, crossvein absent. Cup+1A anastomosis position slightly less than halfway between origin and Cu fork. 2A and 3A well-developed, fused a short distance before separating and continuing to posterior wing margin at axillary angle. Anal area with several irregular veinlets and crossveins. Anal angle slightly produced. Posterior margin distad of angle slightly concave to first third of cubital area, then continuously convex to wing apex, posterior margin slightly emarginate at Mp_1 and Rs_2. *FW maculation*. Extremely pale, almost nonexistent. Very pale macula present in proximal third of cubital area, near apical curve of mediocubital area, several adjacent to that in postsectoral area, a few in distal portion of radial area and apical area near compressed domain. Male apical pigment patch characteristics unknown. *Hind wing*. Costal area not expanded in basal part of wing, essentially parallel from near base to pterostigma. Pterostigma comprising six branched and unbranched veinlets, opaque membrane pigment occupying portions of six to seven cells. Apical area containing three to four branched and unbranched veinlets, with six to seven crossveins. Sc space with seven crossveins in distal third. Four to five presectoral crossveins. Medial triangle with four pre-fork crossveins; distal domain comprising two elongate cells. Two to three triangular marginal cells present. Posterior wing margin convex in anal area, straight until medial triangle, convex until wing apex, very slightly emarginate at Mp_1 and Rs_2. *HW maculation*. As in FW.

Abdomen. Outlines of T2+T3 and S3 diverging distad; outlines of T4–T6 and S4–S6 converging. T1 very pale brownish yellow with brown maculation on integument as bases of setae; T2 and T3 dark brown laterally and very pale brown dorsally, distal margins with a narrow transverse dark brown macula, T3 also with a diffuse transverse dark brown macula mesally; T4–T8 brown, distal margins subapically pale brown; all tergal surfaces bearing very fine golden microtrichia, appearing prunescent; S2 proxomesally and laterally dark brown otherwise very pale brown, S3–S5 dark brown in proximal two-thirds, distal third pale brown, remaining sternites obscured in specimen. T1 bearing long, very slender, brown and white setae; T2–T3 bearing very sparse long white, very slender, setae, slightly denser laterally; S2–S3 bearing long, very slender, brown setae, denser laterally; pleural membrane of segments 2–3 with a thick coat of medium long thin white setae. Ectoprocts dark brown mesally, otherwise with very pale yellowish brown mottling. *Sexually dimorphic characteristics*. *Males*. Unknown. *Females.* T9 dark brown mesally, otherwise very pale brown.

Male terminalia. Unknown.

Female terminalia (A1 Figs. 37, 38). Distivalvae small, globose, fused mesally, with little space between them, setae on ventral surfaces long. Membrane between para-linguellar folds and T8 plates with setae short and somewhat sparse. Linguella dorsal bulb medium large. Interdens slightly larger, slightly wider than long, slightly wedge-shaped. Ventrovalvae medium in size, somewhat shallowly invaginated dorsally, dorsally with long apically hooked slender black setae, mesolaterally with short black robust setae, ventral setae slightly longer and more slender.

Variation. For several of the diagnostic features of the single individual examined, it is impossible to know which represent true autapomorphies of the species and which are merely specimen-level anomalies. But comparison with variation seen in other species provides some clues. The large size of the cells subtending R, for example, is a feature also seen in *A. maynei*; in that species, size of cells varies somewhat among specimens, but is nevertheless generally larger than in other species; the character probably occurs in a similar manner for *A. albus*. Some features of the *albus* specimen, however—the lack of mesothoracic velvety spots and the emarginate FW apices—have no parallel in the genus. It is possible that they represent developmental anomalies such as inadequate pupal development and/or incomplete wing expansion after eclosion (although the color of the velvety spots appears to be an expression of the structure of the microtrichia, and not related to tanning of sclerites). Until further material is collected and examined, these characteristics can only be recognized as unique. The faintness of the expression of maculation throughout the wings may indicate the specimen is teneral. In spite of these uncertainties, the specimen expresses a unique combination of characteristics that clearly set it apart as a new species (e.g, annulated antennae, dense white thoracic setae, produced FW anal angle, open wing venation, etc.).

Natural history and immature stages.—Nothing is known about the biology of this species.

Primary type.—

Allocormodes albus n. sp.

—Holotype by present designation, ♀, BMNH (A1 Fig. 35–38). *Type locality*: Angola, Congolo (region) [-8.450000°, 20.833333°], 859 masl. *Label data*: "ANGOLA: Congulu. iv.1934. K.Jordan. B. M. 1934-435. /// HOLOTYPE Allocormodes albus Jones ♀ design. J. R. Jones 2013 /// JRJ_01205". *Condition*: excellent; antennae and wings spread, no parts missing, antennae and left HW attached with glue; abdomen dissected at 5th segment, dissected tissues, including lateral body walls of terminal segments and genital cavity around linguella, torn.

Additional material examined.—None.

Discussion.—As with all species known from a single individual, the decision to describe them or not often hinges upon the uniqueness and quality of the specimen. In this species, the specimen is in excellent condition, and many features vouch to its singularity within the genus, as noted under *Variation* above. However, some of its characteristics may indicate the specimen is teneral (i.e., pale wing maculation pattern) and/or anomalous (i.e, emarginate FW apical margins).

This species shares a close relationship with *A. lefebvrei* and *A. kolbei* based on the unexpanded costal areas, the presence of antennal setitori, the cream colored pterostigmata, the developed anal angle of the FW, the narrowed wing bases and the white body setae.

The absence of mesoscutal velvety spots is unique for the genus.

Allocormodes inconspicuus *n. sp.*

(A1 Figs. 39–46, 94b, 120)

Etymology and nomenclatural notes.—from *inconspicuus* (Latin), ‘not readily visible, not prominent’; adjectival. This species is named for its unremarkable appearance, which precluded its immediate recognition as a unique entity.

Diagnosis.—Cervical sclerite very pale dull brown; thorax integument brown with only weakly expressed paler patterning dorsally; fore- and hind wing pterostigmata pigmentation weakly expressed, only very pale cream and speckled brown, translucent;

wing maculation a long narrow broken mesal band following the long axis of the wing; male forewing pigment patch devoid of pigment, essentially absent.

Proposed autapomorphies.—No autapomorphies were recovered in the cladistic analysis for this species.

Distribution (A1 Fig. 120).—Central Africa: Burundi, Democratic Republic of the Congo.

Description.—

Size (mm). Male: body length 28, abdomen 15, forewing 34, hind wing 29, antennae 23. Female: body length 33, abdomen 21, forewing 38, hind wing 34, antennae 24.

Head. Occiput glossy, amber brown with yellow and reddish markings. Postorbital sclerite dull to very dark yellowish brown. Vertex pattern slightly asymmetrical from side to side; lateral plates large, well-developed, some with somewhat diffuse edges, yellowish brown, dark regions bearing a sparse coat of long, very slender, dull yellow setae. Anterior extra-torular sclerites very pale yellow. Frons medium dark brown, setae dark brown. Clypeus brown with yellow across surfaces above transverse grooves, setae dark brown. Paraocular band dark brown. thinly and diffusely yellow near mandible bases. Anterior tentorial pit closed. Posterior genal triangle dull orangish brown. *Mouthparts*. Labrum brown to dark brown, setae dark brown. Mandibles dull translucent brown, bearing medium length thin dark brown setae, apices very dark reddish brown.

Maxillary stipes and palpomeres oranish yellow to dusky yellow brown, stipes and palpomere 1 setae dark brown. Labium: submentum and mentum dull yellow brown, setae dark brown; labial palpi amber to reddish brown; ligula dusky yellowish brown. *Eyes*. Golden brown. *Antennae*. Scape dark brown, setae dark brown. Pedicel brown, distal margin an orange ring. Flagellum with 27–29 flagellomeres, entire flagellum evenly yellowish brown, very slightly darker posteriorly and distally, setitori essentially undeveloped. Club with 10–11 flagellomeres, color dark brown in female, male with a thin diffuse dark longitudinal line anteriorly, posterior half pale yellow, anterior surface with a small diffuse pale yellow macula.

Thorax (A1 Fig. 41). *Cervix*. Dorsal cervical plates dark brown, setae brown. Cervical sclerite very pale brown, anterior subapical setae brown. Ventral cervical plate oblong, dusky pale brown, setae brown. *Pronotum*. Entire surface with long, very slender, brown setae. Prescutum brown, median sulcus with a broad orange sagittal stripe, laterally orange. Scutum brown, posterolateral knob dark brown. Scutellum brown, median sulcus with a narrow orange stripe, posterior and lateroanterior margins orangish. *Mesonotum*. Prescutum lobes steeply rounded, dark brown, with a round orangish brown spot on posterior surface and another on anterolateral surface of each lobe, entire surface bearing long, very slender, gray setae in male, long, very slender, dark brown setae in female. Scutum dark brown, with a thin orange ring surrounding velvety spot and in male a long orange stripe posterad of it, surfaces bearing medium short gray setae in male, long, very slender, dark brown setae in female. Scutellum dark brown, laterally orange, in male posterior swelling with a broad orange sagital stripe, in male dorsal surfaces bearing medium long thin, very slender, dark brown and gray setae and posterior margin with a fringe of pale gray setae, in female entire surface with long, very slender, brown setae. Subscutellum dark brown. Postnotum dark brown, glabrous. *Metanotum*. Paraprescutum dark brown, posteriorly diffusely orangish, glabrous. Prescutum dark brown, laterally with long, very slender, setae, thick pale gray in male, very slender, dark brown in female. Scutum dark brown, mesally with diffuse orangish macula, microtrichia dark cinnamon brown, lateral surfaces bearing thick long, very slender, white setae. Scutellum dark brown with lateral diffuse orange macula, sagitally glabrous, parasagittal surfaces bearing long thick gray setae in male, long, very slender, dark brown setae in female. *Pleuron*. Pleurites evenly brown, pleuron bearing a moderately thick coat of long, very slender, dark brown setae, mesothoracic subalar setae thick, white.

Legs. Coxal setae brown. Femora and tibiae orangish to reddish brown, tibiae with some reddish brown spots at bases of setae, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long stiff black; FV: medium short slender stiff black; FAL: medium long slender stiff black; FPL: long stiff black; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow; TPL: long thin stiff black; *mesothoracic leg setae*: FD: long stiff black; FV: stiff medium long black; FAL: mixed medium short and long thin black; FPL: long stiff black; TD: medium length stiff black; TV: long stiff black; TAL: medium length stiff black; TPL: medium length stiff black; *metathoracic leg setae*: FD: mixed very short slender black and some long slender black; FV: long slender black; FAL: long stiff black; FPL: some long stiff black; TD: short stiff black; TV: medium long stiff black; TAL: medium long stiff black; TPL: short stiff slender black. *Tarsi*. Orangish brown.

Wings (A1 Figs. 39, 40, 4294b). All longitudinal and major veins brown, some translucent, most remaining veins, veinlets and crossveins brown, some pale dull yellow, all yellow in anterior portion of apical area. Rs with three or possibly four clear forks. Ambient vein and axillary cord setae white. *Forewing*. Costal area slightly expanded in proximal third of wing, slightly moreso in male, gradually narrowing such that C and Sc become approximately parallel past midpoint to pterostigma. Pterostigma comprising five to six unbranched and branched veinlets, pigment very weakly expressed, particularly in female, proximal three to four cells with reddish brown margining, in male distal three to four cells with very pale cream translucent pigment. Apical area containing five branched and unbranched veinlets, with 14 to 19 crossveins. Sc space without crossveins in male, female with a single crossvein distally. Seven to eight presectoral crossveins. Cubital triangle with four to five sometimes irregular pre-fork crossveins in male, seven to eight in female, distal domain comprising four sometimes irregular cells. A single triangular or trapezoidal marginal cell present. Cup+1A anastomosis position slightly more than half distance from origin to Cu fork. 2A+3A diverging into one or more irregular forks in proximal third of anal area. Anal area with veinlets and crossveins more-or-less regular, oblique. Anal angle essentially straight, ca. 45 degrees of wing axis, in male slightly flatter with apex evenly curving, in female more slightly produced. Posterior wing margin immediately distad of anal angle broadly and very shallowly convex in male, very slightly concave in female, broadly convex from cubital area to wing apex, posterior margin slightly emarginate at Mp_1 and slightly at Rs_1. *FW maculation*. Conspicious margining on crossveins of anal area, distal half of cubital triangle, in proximal half and distal fourth of cubital area, in distal portions of post-sectoral and radial areas, all maculation arranged in a loosely organized longitudinal band. Male apical pigment patch (A1 Fig. 42) area completely devoid of pigment, veins, veinlets and crossveins yellow. *Hind wing*. Costal area slightly expanded in proximal fourth of wing in male, in proximal fifth in female, then narrowing such that C and Sc become approximately parallel to pterostigma, expanding again slightly at pterostigma in male. Pterostigma comprising six to seven mostly unbranched veinlets, pigmentation as in FW. Apical area containing three to four mostly unbranched veinlets, with 14 crossveins in male, 18 in female. Sc space without crossveins in male, female with one to three. Three to five presectoral crossveins. Medial triangle with four pre-fork crossveins in male, five to six in female; distal domain with five cells in male with apex blunt, in female three to four with apex acute. Two or three irregular trapezoidal or triangular marginal cells present. Posterior wing margin immediately distad of anal angle broadly and very shallowly convex in male, very slightly concave in female, broadly convex from posterior medial area to wing apex, posterior margin slightly emarginate at Mp_1 and Rs_1. *HW maculation.* Maculation expressed primarily as two aggregates of longitudinally-aligned margining and membrane pigment, one an ovoid spot overlapping distal part of anterior medial and post-sectoral areas, and the second an elongate one in radial area; a third very small spot in apical area.

Abdomen. Outlines of T2+T3 and S3 diverging distad; outlines of T4–T5 and S4–S5 converging. Tergites and sternites dark brown, distal margins of S3–S7 slightly paler. T1 and T2 with long, very slender, brown setae, but very sparse on T2, T3 dorsally with long, very slender, dull white setae in proximal half; S2–S3 with long, very slender, brown setae more sparse on S3; pleural setae of segments 2–3 long, wispy, dark brown. Ectoprocts dark brown, slightly paler mesally. *Sexually dimorphic characteristics*. *Males*. S9 posterior margin not projecting forward, squared. Pulvini protruding, brownish orange. *Females*. T9 dark brown.

Male terminalia (A1 Figs. 43, 44). 9th sternite posterior margin not projecting forward, square. Gonarcus dorsum distinctly arched subapically in lateral view. Paramere stem not especially darkened, narrow basally, reaching base of gonarcus, blades projecting beyond pelta almost half length of gonarcus, apicoventral margins projecting ventrad of paramere stem, recurving strongly, not widely splayed laterad in distal view. Pelta conspicuous, almond-shaped, mesally depressed, ventrally acuminate, mesal pores numerous. Pulvini somewhat narrow, approximately one and a half to two times longer than width at base, widely separated, bearing long, stiff, slender brown setae, mesally glabrous. Gonosaccal membrane between pulvini with some setae mesally and ventrolaterad of parameres. Hypandrium internum a short broad cone.

Female terminalia (A1 Figs. 45, 46). Distivalvae small, oblong, fused mesally and very proximate. Membrane between para-linguellar folds and T8 plates with setae very dense, medium long, dark brown. Linguella dorsal bulb medium, setae long, robust, apically curved, dark brown, ventral sagittal ridge of tissue not developed. Interdens medium large, sclerotized, slightly longer than wide, slightly wedge or spoon-shaped, apically weakly bilobed. Ventrovalvae medium large in size, moderately invaginated dorsally; setae along dorsal margin medium short, robust, apically curved and hook-like, dark brown, gradually shortening to become very short and peglike subapically; immediately ventrad of peg-like setae, a broad thick transverse band of very short, slender black setae; ventral half of ventrovalve surface bearing a thick covering of medium length, robust but slender black setae.

Variation. Most of the slight differences observed between the only known male and females of *A. inconspicuous* seem to follow those seen in other species, for example the shape of the expansion of the costal areas of the wings, and the length and number of veinlets and crossveins within the cubital and medial triangles and the apical areas. It is somewhat unique for the male to lack Sc space veinlets but the female to have them. However, the female has very few, and the number varies from left wing (3) to right wing (1), and in at least one other species the female regularly has more veinlets than the male (*A. intractabilis*). The difference in color, length and density of the pterothoracic tergal setae between the two specimens is also somewhat peculiar, but appears to a lesser degree in other species as well (e.g., *A. maculipennis*). More specimens are needed to evaluate the range of intraspecific and intragender phenotypic variation for this new and inconspicuous species.

Natural history and immature stages.— The larvae of *A. inconspicuus* have not been described and are unknown.

Primary type.—

Allocormodes inconspicuus n. sp.

—Holotype by present designation, ♀, CAS (A1 Fig. 40). *Type locality*: Democratic Republic of the Congo, 121 km W Popokabaka (town) [-5.692145°, 15.495156°], 277 masl. *Label data*: "B. CONGO: 75 mi. W. of Popokabaka VIII-2-57 /// E.S.Ross & R.E.Leech collectors /// HOLOTYPE Allocormodes inconspicuus Jones ♀ design. J. R. Jones 2013 /// JRJ_00020". *Condition*: excellent; antennae and wings spread; some thoracic hair matted; abdomen apex removed at apex of 5th segment, dissected, genitalia in attached vial.

Additional material examined (paratypes).—Burundi: 1 male [RMCA: JRJ_01191 (A1 Fig. 39)]. Democratic Republic of the Congo: 1 female [RMCA: JRJ_01172].

Discussion.—Of all the species observed in this study, this one, perhaps, expresses the fewest conspicuous diagnostic features, and thus its name. The pale pterostigma and lack of pigment in the FW apical patch area of males seem to be unique characteristics of *A. inconspicuus*.

Allocormodes intractabilis ***(Walker, 1860)***

(A1 Figs. 22, 24, 25, 47–55, 120)

Ascalaphus intractabilis Walker, 1860

—Walker 1860 r#6195: 196 {OD: ♀. TS: not indicated [holotype]. TL: "West Africa". TR: BMNH. Type specimen examined (see "Primary types", below).}

Cormodes intractabilis (Walker, 1860)

—McLachlan 1871.09.14 r#353: 239 {RD: ♀}

Allocormodes intractabilis (Walker, 1860)

—Gerstaecker 1894 r#2559: 100 {DIS, RD: ♂♀, SYN}

—van der Weele 1909.01.05 r#420: 71, figs. 39, 40 {GD, RD: ♂♀, SYN, TR, TS}

—Soldanski, H. 1912 r#5787: 119{BIO, DIS, GD, FP, SYN}

—Navás 1925 r#795: 123 {SR}

<u>Etymology and nomenclatural notes</u>.—from *intractabilis* (Latin), 'unmanageable, rough, intractable'; adjectival. No reason for the name selection is given in the original description, but it may refer to the thick coat of white setae covering the thorax and base of the abdomen.

Gerstaecker (1894) designated *Haploglenius maculipennis* Taschenberg as a synonym of *A. intractabilis*, but van der Weele (1909) suggested that Gerstaecker must have only read the description of *A. maculipennis* and not seen specimens, and retained *A. maculipennis* as a separate species.

Diagnosis.—Lateroposterior setae on pterothorax and base of abdomen long, white; mesothoracic velvety spots present; costal area of hind wings slightly to conspicuously expanded basally; FW anal area not produced; FW pterostigma color cream and brown; wing maculation a single axial interrupted brown line; male apical pigment patch broad, often reaching proximally to Mp_1; overall size large.

Proposed autapomorphies.—No unambiguous autapomorphies were recovered in the cladistic analysis for this species.

Distribution (A1 Fig. 120).—Western sub-Saharan tropical belt: Democratic Republic of the Congo, Equatorial Guinea, Gabon, Ghana, Ivory Coast, Liberia, Nigeria, Uganda. In addition to the localities confirmed from loan specimens, van der Weele (1909) mentions having seen specimens from Sierra Leone.

Description.—

Size (mm). Male: body length 30 (24–37), abdomen 15 (11–20), forewing 41 (37–45), hind wing 35 (31–37), antennae 29 (23–32). Female: body length 30 (27–32), abdomen 18 (15–22), forewing 45 (42–48), hind wing 41 (37–43), antennae 30 (28–32).

Head. Occiput dull yellow to dark reddish brown, darker near cervix, distal margins paler, yellowish. Postorbital sclerite variable in color from pinkish to yellowish brown to dark brown. Vertex pattern variable, lateral plates variable in shape, dull yellow to pale brown, dark regions bearing a silvery micropile, often indistinct and/or obscured by long, very slender, white setae. Anterior extra-torular sclerites cream to amber yellow. Frons yellowish brown, setae brown. Clypeus amber-brown, setae brown. Paraocular band dull yellowish to reddish brown, slightly darker in some females. Anterior tentorial pit often open ventrally as a small round pore. Posterior genal triangle dull orangish to reddish brown. *Mouthparts*. Labrum amber-brown to brown, setae golden brown. Mandibles very dull brown basally, reddish brown subapically, apices dark brown. Maxillary stipes and palpomeres amber or reddish brown, stipes and palpomere setae brown. Labium: submentum and mentum dull reddish or brownish yellow, setae brown; labial palpi amber to reddish brown; ligula pale to yellowish brown. *Eyes.* Golden brown. *Antennae.* Scape reddish brown to brown, setae dark brown. Pedicel orange to brown. Flagellum with 28-31 flagellomeres, brown to pale brown with pigment paler at flagellomere base immediately after slightly darker node, node itself sometimes paler, setitori absent to somewhat developed in distal half of flagellum. Club with 9-12 flagellomeres, color brown, sometimes paler yellow-brown ventrally.

Thorax (A1 Fig. 50). *Cervix*. Dorsal cervical plates pale yellow to brown or patterned with both colors, setae white. Cervical sclerite brown, subapical dorsal setae brown. Ventral cervical plate knob elongate, very pale brown, setae brown. *Pronotum*. Setae somewhat numerous, long, wispy, pale brown and white. Prescutum yellow to brownish, with sublateral dark brown maculation. Scutum mediodorsally yellow, with faint sublateral brown flecking, ventrolateral knob reddish brown to dark brown with irregular sublateral pale brown maculations. Scutellum yellow, with a narrow dark brown transverse medially-divided dorsal stripe, bearing numerous long, very slender, brown and white setae. *Mesonotum*. Prescutum dull brown, slightly paler at dorsum of each lobe, darker anteriorly, yellowish anterolaterally, bearing long, very slender, dark brown setae dorsally and thick long white, very slender, setae anterolaterally. Scutum very dark brown, area around spot yellowish, a yellowish stripe often extending posteriorly from near mesal margin of spot, remaining surfaces an irregular and variable pattern of yellow and brown, dorsal and sublateral surfaces bearing sparse, very slender, brown setae, lateral surfaces bearing a thick coat of long, very slender, white setae. Scutellum pattern variable, yellowish to brown anteriorly, brown posteriorly, often a yellow stripe extending laterally from midpoint, and another yellow stripe following along midline, posterior swelling yellow, dorsal surfaces bearing few long, very slender, brown setae, lateroposterior surfaces bearing a thick coat of long, very slender, white setae. Subscutellum color. Postnotum yellowish to brown but obscured under setae of scutellum. *Metanotum*. Paraprescutum yellow and brown, obscured by posterior fringe of white setae of metascutellum and forewing axillary cord. Prescutum yellow anteriorly, orangish brown posteriorly, with a median transverse brown stripe bearing sparse long erect brown setae. Scutum microtrichia brown, color pattern obscure, mixed yellow and brown, lateroposterior margins bearing thick coat of long white setae. Scutellum posterior margin yellow, with large round sublateral brown maculae, posterolateral surfaces covered with long, very slender, white setae. *Pleuron*. Pleurites evenly brown, bearing a thick coat of long, very slender, white and sometimes brown (in subalar and prothoracic regions) setae.

Legs. Coxal setae brown and dull white. Femora and tibiae more-or-less evenly brown, sometimes yellowish, metathoracic tibia brown in proximal third, pale brown to yellow in distal two-thirds, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: medium long stiff dark brown; FV: short slender stiff black and white; FAL: short slender stiff black and white; FPL: numerous long stiff black mixed with moderately thick long slender white; TD: medium long stiff black; TV: short stiff black; TAL: preening patch setae golden yellow; TPL: numerous long stiff black intermingled with medium long stiff slender black; *mesothoracic leg setae*: FD: long slender white; FV: proximally sparse, very slender, white; FAL: proximally sparse very short stiff black; FPL: numerous long stiff black; TD: mesolongitudinally glabrous; TV: long stiff slender black; TAL: short stiff black; TPL: short stiff black; *metathoracic leg setae*: FD: sparse short slender black and white; FV: proximally sparse, very slender, white; FAL: long, very slender, white and distally a few medium length stiff black; FPL: numerous long stiff black intermingled with long, very slender, white; TD: mesolongitudinally glabrous; TV: long stiff slender black; TAL: numerous very short appressed stiff black; TPL: short and medium length stiff black. *Tarsi*. Reddish brown.

Wings (A1 Figs. 22, 24, 25, 47, 49, 51). Apices in males subacute, in females slightly more rounded. Major longitudinal and many crossveins reddish brown; many veinlets and crossveins in post-sectoral, cubital and anal areas yellow. Rs with three clear forks.

Ambient vein and axillary cord setae mixed white and brown. *Forewing*. In males, costal area slightly expanded in proximal third, then gradually narrowing such that C and Sc become approximately parallel just past midpoint until immediately preceding pterostigma, when area expands again; in females, costal area slightly expanded in proximal fifth, then gradually narrowing such that C and Sc become approximately parallel for distal two-thirds of wing to pterostigma. Pterostigma longer in males, comprising six or seven mostly unbranched veinlets and seven or eight cells, veins and cells opaque cream yellow, opaque membrane pigment commencing three to four cells basad of Sc-R anastomosis; in females shorter, comprising five to seven mostly unbranched veinlets and six to eight cells, opaque membrane pigment commencing two to three cells basad of Sc-R anastomosis; veins and cells opaque cream yellow, darkened with granular reddish brown pigment on anterior portions, proximal two to three veinlets and cells often quite dark. Apical area containing four to six branched and unbranched veinlets, with ca. eight to fifteen crossveins. Sc space with five to fifteen crossveins in distal half. Five to eight presectoral crossveins. Cubital triangle with four to six prefork crossveins; distal domain comprising three to five irregular cells. One triangular marginal cell present. Cup+1A anastomosis position nearly at cubital fork. 3A well-developed, fusing with 2A a short distance before separating and continuing to posterior wing margin. Several irregular curving crossveins connecting 1A, 2A and 3A. Anal angle ca. 45 degrees of wing axis, essentially straight. Posterior wing margin distad of angle unexcavated and even or very slightly convex in males, in females unexcavated and even or very slightly concave. *FW maculation*. Maculation consisting of a more-or-less straight line of interrupted brown marginations on veinlets and crossveins, traveling wing axis from anal area and cubital triangle to wing margin in compressed domain of subapical field region, a small maculation occasionally positioned in apical area. Male apical pigment patch (A1 Fig. 51) occupying one-fifth to one-fourth of wingtip, pigment proceeding posteriorly from pterostigma nearly to posterior wing margin, distal portions covering anterior area of apical area, proximal edges fading into margining of veinlets and crossveins in distal portions of post-sectoral area. *Hind wing*. Costal area expanded in proximal sixth, more abruptly than in forewing, then gradually narrowing such that C and Sc become approximately parallel at midpoint until immediately preceding pterostigma, when area expands again. Pterostigma longer in males, both sexes with veins and cells opaque cream yellow, darkened with granular dark reddish brown pigment on anterior portions, proximal two to three veinlets often quite dark. Apical area containing three to four branched and unbranched veinlets in males, four to five in females, with ca. six to ten crossveins in males and ca. eleven to sixteen crossveins in females. Sc space with five to ten crossveins in distal half in male, nine to seventeen veinlets in distal half in female. Three to six presectoral crossveins. Mp_1 and Mp_{2a} often appearing to fuse near hind wing margin. Medial triangle with four to seven pre-fork crossveins, occasionally with one to several crossveins in fork area; distal domain comprising three to five cells. One to two narrowly trapezoidal or triangular marginal cells present. Anal area slightly more expanded in male than in female. Anal area of males not reduced, well developed, unexcavated, in females less expanded, post-angle margin very slightly excavated. Posterior wing margin of posterior medial area slightly excavated mesally in male, even or very slightly concave in female. *HW maculation*. Maculation similar to that in forewing, but line most strongly expressed in distal half of wing, a few cells completely filled with pigment, and apical area maculation apparently always present.

Abdomen. Outlines of T3 and S3 diverging distad; outlines of T4–T5 and S4–S5 converging. Proximal margins of segments darkened, distal margins paler, some with yellow maculations on sternites, particularly S3. T1 to proximal half of T3 and S1–S3 completely covered with long white setae; pleural setae of S2–S3 thick, chocolate brown. Ectoprocts brown apically, yellow laterally. *Sexually dimorphic characteristics*. *Males*. Abdomen short, usually about one-third, but as much as one-half hind wing length; segments 6-8 narrow. Tergal white setal coat thick. Pulvini not protruding, dark reddish brown. *Females*. Abdomen longer than in males, usually about one-half but as short as one-third hind wing length; segments 6-8 sometimes slightly narrowed. Tergal white setae coat somewhat sparse. T9 dark brown basally, yellowish distomesally.

Male terminalia (A1 Figs. 52, 53). 9th sternite posterior margin projecting forward slightly, subacute. Gonarcus dorsum only very slightly arched in lateral view. Paramere stem darkened nearly to base, not narrowed, blades projecting beyond pelta one-third length of gonarcus, apicoventral margins projecting ventrad of paramere stem but not recurving, splayed laterad in distal view. Pelta conspicuous, almond-shaped, mesally depressed, ventrally subacuminate, mesal pores numerous. Pulvini length one to two times width at base, widely separated, bearing medium-long, stiff, slender brown setae on all surfaces. Gonosaccal membrane between pulvini bearing numerous long, stiff, slender setae. Hypandrium internum pouch weakly sclerotized anterior and posteriorly, anteriorly trilinear, posteriorly v-shaped.

Female terminalia (A1 Figs. 54, 55). Distivalvae small, swollen clamshell-shaped, slightly separated. Para-linguellar folds as in other species. Linguella dorsal bulb medium-sized, ventrally with a sagittally-raised ridge of tissue. Interdens small, tab or spoon-shaped, very flat and thin, slightly convex, with a very fine apicosagittal line. Ventrovalvae large, deeply invaginated dorsally, mesal surfaces bearing a medium-short stiff curved brown setae.

Variation. One male (JRJ_00008) lacking Sc space veinlets in right forewing. One specimen (JRJ_01154) spiracle 5 trachea with internal, dark brown, sclerotized mass coursing throughout trachea, branching and following twists and turns; its identity is unclear, but it is unlikely to be a gland, as it is not seen in other specimens nor other species, nor a strange nematode, as it branches repeatedly.

Natural history and immature stages.—Soldanski (1912) examined five females Alen, Equatorial Guinea collected 27 April, 14, 24 and 25 September, and 2 December 1906 (all re-examined here; from MFNB). The first four of these were collected on trees during general collecting, based on data from Tessmann, the collector. Soldanski suggested that due to the span of the collecting dates, the species might be bivoltine. The fact that four separate females were collected while resting on trees suggests that adult females may frequent arboreal perches, and it may be that they prefer trees to grasses and shrubs.

Allocormodes in general seem to be uncommonly collected. But, in loan material borrowed for this study, *A. intractabilis* was the most frequently encountered species, with males and females occurring in about equal numbers. Label dates indicate that both sexes are present throughout the known flight period, from late November to mid-August (see A1 Excel file 1).

Allocormodes intractabilis adults may be attracted to lights. One label reports a male collected July 10 1954 in Uganda at a mercury vapor light in a *Glossina* thicket (JRJ_00005: see A1 Excel file 1). The larvae of *A. intractabilis* are unknown.

Primary type.—

Ascalaphus intractabilis Walker, 1860

—Holotype ♀, BMNH, examined (A1 Fig. 48). *Type locality*: West Africa (no further information available). *Label data*: "W. Afr.", no JRJ database number attached. *Condition*: excellent; wings spread, antennae, legs, wings, abdomen attached, right HW with large piece of posterodistal margin missing.

The holotype specimen was examined briefly and photographed during a visit to The Natural History Museum (BMNH), but not borrowed on loan for further examination.

Additional material examined.—*Democratic Republic of the Congo*: 2 males, 4 females [CAS: 1 female, JRJ_00015; NMW: 1 male, 1 female, JRJ_00001, JRJ_00018; RMCA:

1 female, JRJ_01160; SDEI: 1 male, JRJ_01154; USNM: 1 female, JRJ_00012]. *Equatorial Guinea*: 3 females [MFNB: JRJ_00011, JRJ_01156, JRJ_01157]. *Gabon*: 2 males, 1 female [CMNH: JRJ_00003 (A1 Fig. 47), JRJ_00004, JRJ_00009]. *Ghana*: 2 females [ARC: 1 female, JRJ_00016; BMNH 1 female, JRJ_00017]. *Ivory Coast*: 1 male, 3 females [CIRAD: 1 male, 2 females, JRJ_00002, JRJ_00013, JRJ_00014 (A1 Fig. 49); MFNB: 1 female, JRJ_00010]. *Liberia*: 2 males, 1 female, [CMNH: Liberia, JRJ_00006, JRJ_00007, JRJ_00019]. *Nigeria*: 1 male [USNM: JRJ_00008]. *Uganda*: 2 males [BMNH: JRJ_00005; SDEI: JRJ_01155].

Discussion.—This is a widely distributed, commonly collected, and readily-diagnosable species.

Allocormodes junodi *van der Weele*

(A1 Figs. 33, 34, 56–64, 120)

Allocormodes junodi van der Weele

—van der Weele 1909.01.05 r#420: 73, fig. 42 {OD: ♂♀, DIS, ET. TS: not indicated [syntypes: 1♂, 2♀♀; a lectotype needs to be designated from syntype material]. TL: “Transvaal”. TR: NAVC (♂), “Genfer Museum” [MHNG] (♀♀). Syntype examined (see “Primary types”, below).}

Etymology and nomenclatural notes.—*junodi*: a Latinized noun in the genitive case (Art. 11.9.1.3), named by van der Weele (1909) for the reverend Mr. Junod, a collector of African insects and collector of the type specimen.

Diagnosis.—Costal area of hind wings slightly to conspicuously expanded basally; hind wing with a distinct brown macula positioned at apex of medial triangle (convergence of Mp_{2p}, Cua, and bases of veins forming marginal cells); thoracic setae brown; medium size.

Proposed autapomorphies.—Setal spots present at base of most setae on flagellomere internodes in distal half of antennae; outline of HW margin proximad of marginal cell(s) convex in females; a distinct brown macula positioned at convergence of Mp_{2p}, Cua, and bases of veins forming marginal cell.

Distribution (A1 Fig. 120).—Western margins of southeastern tropical corridor: Malawi, South Africa.

Description.—

Size (mm). Male: body length 35, abdomen 19, forewing 38, hind wing 32, antennae 22. Female: body length 32, abdomen 19, forewing 43, hind wing 39, antennae 25.

Head. Occiput brown. Postorbital sclerite amber brown. Vertex pattern variable, obscured in female specimen, in male specimen shape of lateral plates asymmetrical from side to side, dark regions bearing long, very slender, brown setae. Anterior extra-torular sclerites pale to amber yellow, with a dark internal costa visible at line of mesal fusion. Frons brown, setae brown. Clypeus brown, setae brown. Paraocular band brown, darker along eye margin. Anterior tentorial pit closed. Posterior genal triangle brown. *Mouthparts*. Labrum brown, setae dark brown. Mandibles very dull brown basally, reddish brown subapically, apices dark brown. Maxillary stipes and palpomeres amber or reddish brown, stipes and palpomere setae brown. Labium: submentum and mentum setae brown; labial palpi amber to reddish brown; ligula pale to yellowish brown, ventrally with a faint narrow median longitudinal dark brown stripe. *Eyes.* Golden brown. *Antennae.* Scape reddish brown to brown, setae brown. Pedicel orange to brown. flagellum with 28-31 flagellomeres, yellow to brown with pigment paler at flagellomere node, darker in area immediately subtending node, setitori very weakly expressed. Club with 12 flagellomeres, color dark brown formed by pigment spot at base of each short black seta, remaining areas yellow.

Thorax (A1 Fig. 59). *Cervix*. Dorsal cervical plates dark brown, setae brown. Cervical sclerite yellow to pale brown, subapical setae brown. Ventral cervical plate knob ovoid, very pale brown, setae brown. *Pronotum*. Setae somewhat numerous, long, wispy, brown. Prescutum yellow, with sublateral dark brown maculation. Scutum brown, with some slight yellow flecking posteriorly, posterolateral knob dark brown. Scutellum orangish yellow, with a moderately broad dark brown transverse medially-divided dorsal stripe, bearing numerous long, very slender, brown setae. *Mesonotum*. Prescutum lobes brown to dark brown, with a round yellow spot on posterior surface and another on anterolateral surface of each lobe, entire scutum surface bearing long, very slender, brown setae, with some intermingled white long, very slender, setae laterally. Scutum very dark brown, area anterior and posterior to spot slightly yellowish, a very weak and thin diffuse yellowish stripe extending posteriorly from near mesal margin of spot, remaining surfaces brown, all surfaces bearing, very slender, golden brown setae. Scutellum brown, with a diffuse yellow macula laterally, in female a broad diffuse yellow stripe along median sulcus on posterior transverse swelling, all surfaces bearing long, very slender, brown setae, surfaces bearing a fringe of long, very slender, golden brown setae. Subscutellum brown, in female diffusely yellowish laterally. Postnotum brown. *Metanotum*. Paraprescutum brown, with diffuse mesal yellow maculation, glabrous. Prescutum brown, with sparse long erect brown setae. Scutum brown to dark brown, microtrichia dark brown, lateroposterior margins bearing long, very slender, brown setae. Scutellum brown, in female laterally yellow, posterior margin slightly darker, all except for posteromedial surface bearing long, very slender, brown setae. *Pleuron*. Pleurites evenly brown, bearing a moderately thick coat of long, very slender, brown setae.

Legs. Coxal setae brown. Femora dull yellow to pale brown, in female with dark reddish brown spots at base of all stiff dark setae, these spots also on tibia in both sexes, tibia slightly darker brown dorsally, dull yellow on remaining surfaces, except at setal bases, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long stiff black; FV: short slender stiff black; FAL: short slender stiff black; FPL: long stiff black; TD: mixed short and medium length stiff black; TV: mixed short and medium length stiff black; TAL: preening patch setae golden yellow, except a few short black on proximal margin of patch; TPL: long thin stiff black; *mesothoracic leg setae*: FD: very short stiff black; FV: mixed very long slender black and very long very slender brown; FAL: mixed very long slender black and very long very slender brown; FPL: mixed very long slender black and very long very slender brown; TD: mesolongitudinally glabrous; TV: short slender black mixed with very long stiff slender black; TAL: short stiff black; TPL: short stiff black; *metathoracic leg setae*: FD: very short slender black setae and some long stiff slender black; FV: short slender black; FAL: very short slender black setae and a brief series of aligned, long stiff black; FPL: numerous long stiff black; TD: mesolongitudinally glabrous; TV: short stiff black and long stiff slender black; TAL: short stiff black; TPL: short stiff black. Tarsus medium reddish brown.

Wings (A1 Figs. 56–58, 60). Apices of male very slightly asymmetrical, of females more rounded. Major longitudinal and many crossveins reddish to dark brown; many veinlets and crossveins throughout yellow, many of these brown ventrally. Rs with three clear forks. Ambient vein and axillary cord setae brown. *Forewing*. Costal area expanded in proximal fourth of wing, gradually narrowing such that C and Sc become approximately parallel at midpoint to pterostigma. Pterostigma comprising five or six mostly unbranched veinlets, opaque membrane pigment commencing two to three cells basad of Sc-R anastomosis; in males, pterostigma veins and cells opaque cream yellow; in females, pterostigma veins and cells opaque cream yellow, proximal veins margined with granular brown pigment. Apical area containing five to seven branched and unbranched veinlets, with ca. twelve to twenty one crossveins. Sc space veinlets absent in male, female with one to two veinlets. Six to seven presectoral crossveins. Cubital triangle with five to seven prefork crossveins; distal domain comprising three to five irregular cells. One triangular marginal cell present. Cup+1A anastomosis position nearly at cubital fork in male, in female approximately two-thirds distance from Cup origin to fork. 3A well-developed, fusing with 2A a short distance before separating and continuing to posterior wing margin. Anal area with numerous irregular veinlets and crossveins. Anal angle ca. 45 degrees of wing axis, essentially straight Posterior wing margin distad of angle even or very slightly convex. *FW maculation*. Margination on most crossveins of anal area, a few in cubital triangle, several in anterior and basal posterior portions of cubital area, and a few mesally in apical area; marginations and membrane darkening of several cells forming a diffuse macula in post-sectoral area at the point where Mp_2+ Cua_1 and Mp_1 begin to curve toward posterior wing margin, and another larger and more elongate macula in radial area basad of compressed domain of subapical field (more well-developed in female). Male apical pigment patch (A1 Fig. 60) lacking opaque white pigment on cell membranes, patch expressed instead as cream-yellow veinlets and crossveins in anterior portions of apical and subapical fields. *Hind wing*. Costal area expanded in proximal fourth of wing, then gradually narrowing such that C and Sc become approximately parallel at midpoint until immediately preceding pterostigma, when area expands again very slightly. Pterostigma longer in male than in female, comprising seven to nine mostly unbranched veinlets, opaque membrane pigment commencing three to five cells basad of Sc-R anastomosis, veins and cells proximally darkened with granular brown pigment, distally opaque cream yellow; in female, pterostigma shorter, comprising five to six branched and unbranched veinlets, opaque membrane pigment commencing two to three cells basad of Sc-R anastomosis, veins and cells darkened with granular brown pigment, distal cells opaque cream yellow. Apical area containing four to five branched and unbranched veinlets, with nine to ten crossveins in male and ca. nineteen to twenty-one crossveins in female. Sc space veinlets absent in male, female with one veinlet near anastomosis of Sc and R. Four presectoral crossveins. Medial triangle with four pre-fork crossveins in male, seven in female; distal domain comprising four cells. Three to four narrowly trapezoidal or triangular marginal cells present. Anal area slightly more expanded in male than in female. Posterior wing margin of posterior medial area slightly excavated mesally in male, even or very slightly concave in female. *HW maculation*. Margination on a few crossveins mesally in apical area; marginations and membrane darkening of several cells forming a diffuse macula in post-sectoral area at the point where Mp_{2a} and Mp_1 begin to curve toward posterior wing margin, and another larger and more elongate macula in radial area basad of compressed domain of subapical field (more well-developed in female); distinct small macula at anastomosis of Cua and Mp_{2p}, extending onto base of veins forming marginal cells.

Abdomen. Shape and size of sexes similar, female slightly more robust. Surfaces of T2+T3 and S3 diverging distad; outlines of T4–T6 and S4–S6 converging. Tergum orangish brown with paler orange distal margins, sternum dark brown. Acrotergite 2 without dorsal setae, pleural membrane of segments 2 and base of 3 bearing a coat of brown setae. *Sexually dimorphic characteristics*. *Males*. Distal one fourth of S3 bright orangish yellow. T1 and S1–S3 bearing a thick coat of long, very slender, brown setae;

T2 bearing medium length erect thin white setae; T3 with a dorsal patch of erect thin white setae, medium in length but shortening apicad. Pulvini very slightly protruding, orangish brown. Ectoprocts brown. *Females*. T1 bearing a thick coat of long, very slender, brown setae; S1 to S3 with some thin wiry long brown setae; T2 and basal one third of T3 bearing a dorsal patch of medium length erect thin white setae. Ectoprocts color pattern obscure brown and orange, dark brown basally, yellowish distomesally.

Male terminalia (A1 Figs. 61, 62). 9th sternite posterior margin not projecting forward, nearly square. Gonarcus dorsum arched subapically in lateral view. Paramere stem darkened almost to base, not narrowed basally, blades projecting beyond pelta one-fourth length of gonarcus, apicoventral margins recurved toward stem, somewhat widely splayed laterad in distal view. Pelta conspicuous, broadly almond-shaped, mesally depressed, ventrally blunt, mesal pores conspicuous. Pulvini well-developed, approximately two times longer than width at base, bearing medium-long setae and a few very long stiff, slender brown setae apically, mesal surfaces glabrous. Gonosaccal membrane between pulvini with a few setae. Hypandrium internum surfaces weakly sclerotized.

Female terminalia (A1 Figs. 33, 34, 63, 64). Distivalvae very small, globose, nearly fused mesally, with little space between them. Para-linguellar folds as in *A. intractabilis*. Linguella dorsal bulb large, round, ventral sagittal ridge of tissue undeveloped. Interdens nearly twice as wide as long, slightly flexed sagittally, apex very weakly bilobed. Ventrovalvae medium in size, somewhat deeply invaginated dorsally, mesal surface setae short, black, and very robust.

Variation. The hind wing maculations in van der Weele's (1909) figured female are slightly smaller than in the specimen examined in this study, suggesting intraspecific and intragender variation within this species.

Natural history and immature stages.—Unknown.

Primary types.—

Allocormodes junodi van der Weele

—Lectotype by present designation, ♂, MNHN, examined (A1 Fig. 56). *Type locality*: South Africa, Leydsdorp (a ghost mining town in Limpopo province of South Africa) [-23.995552°, 30.521247°], 674 masl. *Label data*: "MUSEUM PARIS LONGIN NAVAS LEGIT 1927 /// ENVOI DU RÉVÉREND II.JUNOD. /// LEYDSDORP N. TRANSVAAL. 1902. /// Typus /// LECTOTYPE /// Allocormodes junodi VdW det VdWeele /// LECTOTYPE Allocormodes junodi van der Weele ♂ design. J. R. Jones 2014 /// JRJ_01214 /// Allocormodes junodi ♂ det. J. R. Jones 2011". *Condition*: moderate; thorax with two large holes on left side from dermestid damage, all parts still attached, right front wing twisted, torn at Rs to posterior wing margin.

—Paralectotypes, 2 ♀♀, MHNG, not examined. Condition: unknown.

Van der Weele (1909) examined 3 specimens, the MNHN male and two additional females from the Geneva Museum (MHNG), but fixed none as the holotype. The male is referred to by van der Weele (1909) in his original description as being at that time in the

Navás collection. The label reading “Typus” is handwritten on faded red paper in writing that resembles that of Navás, not van der Weele. The first label reading “LECTOTYPE” is typed on bright red card stock. The van der Weele determination label is handwritten in cursive on tan cardstock in van der Weele’s hand. It is not clear who placed the first lectotype label on the male specimen (perhaps Tjeder?). Despite the presence of this label, there does not appear to be any published designation of this specimen as a lectotype, and it is not regarded as such here. The female syntypes were not examined. Van der Weele (1909) gave their locality as “Transvaal” and indicated they were also collected by Reverend Junod.

Additional material examined.—*Malawi* : 1 female [BMNH: JRJ_01211 (A1 Fig. 57)].

Discussion.—*Allocormodes junodi* is uncommonly collected.

Allocormodes kolbei *van der Weele*

(A1 Figs. 65–74, 121)

[*Allocormodes intractabilis* Walker]

—Kolbe 1897 r#3434: 28 {misidentification of ♀ (synonymy designated by van der Weele 1909)}

Allocormodes kolbei van der Weele

—van der Weele 1909.01.05 r#420: 75, figs. 44, 45 {OD: ♂♀, DIS, ET. TS: not indicated [syntypes: 2♂♂, 1♀; a lectotype needs to be designated from syntype material]. TL: "Mhonda, D. Ost-Afrika". TR: MFNB. Syntypes not examined (see "Primary types", below).}

Allocormodes woodi Esben-Petersen **new synonym**

— Esben-Petersen 1927.10.01 r#163: 343, Pl. X fig. 1 {OD: ♀, DIS, ET. TS: not indicated [holotype]. TL: "Nyasaland". TR: BMNH. Holotype examined (see "Primary types", below).}

Identification uncertain (larvae)

—Withycombe 1923 r#14565 {BIO, DIS, H, IMS, MOR, SR}

—Poulton 1923 r#11210 {BIO, DIS, H, IMS, MOR, SYN}

—van Someren 1924 r#6165 {BIO, DIS, H, IMS, SYN}

—Poulton 1928 r#5235 {BIO, H, IMS, SR, SYN}

Etymology and nomenclatural notes.—*kolbei*: a Latinized noun in the genitive case (Art. 11.9.1.3), named by van der Weele (1909) for Professor Hermann Julius Kolbe, the collector of one of the described specimens. *Woodi*: a Latinized noun in the genitive case (Art. 11.9.1.3), named by Esben-Petersen (1927) for R. C. Wood, the collector of the described specimen.

Diagnosis.—Width of costal area of hind wings even throughout length; HW medial fork inside angle acute; post-fork portion of medial triangle long, comprising 2 or more cells; antennae three-fourths forewing length, reaching nearly to pterostigma in males; some males with wings melanistic, darkened; overall size medium.

Proposed autapomorphies.—Pleural setae predominantly brown.

Distribution (A1 Fig. 121).—Central east Africa: Democratic Republic of the Congo, Kenya, Malawi, Tanzania.

Description.—

Size (mm). Male: body length 25 (23–27), abdomen 15 (13–17), forewing 38 (35–41), hind wing 34 (31–35), antennae 29 (26–33). Female: body length 26 (24–28), abdomen 15 (14–17), forewing 40 (35–43), hind wing 37 (31–40), antennae 26 (22–29).

Head. Occiput dull to glossy, dull yellow to brown. Postorbital sclerite color variable but usually similar to that of occiput, dull yellow to amber to dark brown. Vertex pattern variable, posterolateral arms of anterior medial plate often narrow, separated from plate itself, dark regions bearing dense coat of white microtrichia and often a thick coat of long, very slender, white setae. Anterior extra-torular sclerites pale whitish to amber yellow, occasionally brown. Frons brown, setae brown. Clypeus brown to dark brown, often with yellow in transverse grooves, setae brown. Paraocular band brown. Anterior tentorial pit open ventrally as a round pore. Posterior genal triangle brown. *Mouthparts*.

Labrum dark brown, setae dark brown and golden brown. Mandibles very dull brown basally, reddish brown subapically, apices dark brown. Maxillary stipes and palpomeres amber or reddish brown, stipes and palpomere setae brown. Labium: submentum and mentum setae brown; labial palpi amber to reddish brown; ligula dull yellow to amber to reddish brown. *Eyes*. Golden brown. *Antennae.* Scape brown to dark brown, setae brown. Pedicel dark brown with an orange brown distal margin. Flagellum with 28-32 flagellomeres, base color dull yellow to reddish brown, with a narrow dark and then pale ring at each flagellomere node, often only darker ring expressed distally, setitori dark brown and often numerous, giving flagellomeres a dark appearance. Club with 8–9 flagellomeres, dark brown formed by pigment spot at base of each short black seta, remaining areas yellow.

Thorax (A1 Fig. 69). *Cervix*. Dorsal cervical plates yellow posterolaterally, dark brown anteromesally, setae brown and white dorsally, white laterally. Cervical sclerite brown, anterior subapical setae brown. Ventral cervical plate knob ovoid, very pale yellow, setae pale brown. *Pronotum*. Setae somewhat numerous, long, wispy¸ pale brown. Prescutum orangish yellow dorsally, with sublateral dark brown maculation, pale yellow laterally, dark brown ventrolaterally. Scutum mediodorsally dull brown, sublateral area orangish yellow with a brown mesal macula, posterolateral knob dark brown. Scutellum dark brown dorsally but divided mesally by a narrow orangish yellow stripe, orangish yellow laterally, bearing numerous long, very slender, pale white and brown setae. *Mesonotum*. Prescutum lobes dark brown, with a diffuse round yellow macula on posterior surface marked with numerous tiny dark flecks, yellow laterally, entire prescutum surface bearing long, very slender, brown setae. Scutum velvety spots surrounded anterolaterally by a yellow macula, remaining color pattern of brown and yellow irregular and variable, often a pair of diffuse yellow spots present laterally, area posterad of velvety spot a diffuse yellow macula with dark flecks at setae bases, divided medially by a brown macula, remaining surfaces brown, all surfaces bearing, very slender, pale brown and white setae, worn off dorsally in some individuals, posterolateral setae white and more dense. Scutellum brown, with a diffuse yellow macula mesolaterally, posterior swelling brown, divided by a short yellow longitudinal stripe or macula, yellow along posteriormost margin, all surfaces bearing long, very slender, brown and white setae, posterior margin with long, very slender, white setae. Subscutellum brown, diffusely yellowish laterally. Postnotum brown, with parasagittal yellow longitudinal stripes. *Metanotum*. Paraprescutum often obscured by mesonotum setae, brown laterally, orangish yellow mesoposteriorly, glabrous. Prescutum brown, orangish yellow anteriorly, sometimes divided longitudinally by a thin transverse yellow line, glabrous. Scutum brown to dark brown, sometimes with yellow maculae along margins, microtrichia dark brown, lateroposterior margins bearing long, very slender, white setae. Scutellum yellow with a broad dark brown sagittal stripe ending at posterior swelling, anterior surface of swelling sometimes bearing a narrow sublateral transverse brown stripe, surfaces bearing long, very slender, brown and white setae. *Pleuron*. Pleurites mostly brown, but with a somewhat poorly developed longitudinal yellow stripe formed of yellow patches on various pleurites, basisternites usually distinctly orangish yellow, all pleural surfaces bearing a sparse coat of long, very slender, dark, pale and golden brown setae.

Legs. Coxal setae pale brown to whitish. Femora and tibiae pale to dark yellow, occasionally brown, with dark reddish brown spots at setae bases, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long, very slender, white; FV: short slender stiff black; FAL: short slender stiff black; FPL: long, stiff black; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow, occupying almost full length of tibia except at base where are a few medium length black setae; TPL: long thin stiff black; *mesothoracic leg setae*: FD: very short stiff black and some very long, very slender, white; FV: short stiff black; FAL: sparse medium long stiff black; FPL: long stiff black mixed with long slender white; TD: mixed short and medium long stiff slender black; TV: mixed short and medium long slender black; TAL: mixed short and medium long stiff slender black; TPL: mixed short and medium long stiff slender black; *metathoracic leg setae*: FD: very short stiff black and some very long, very slender, white; FV: short stiff black; FAL: sparse medium long stiff black; FPL: long stiff black mixed with long slender white; TD: sparse short slender black and one or two medium long stiff black; TV: short stiff black; TAL: medium long stiff slender black; TPL: medium long stiff slender black. Tarsus orangish yellow, sometimes reddish brown.

Wings (A1 Figs. 65–68, 70). Apices rounded in both sexes. Major longitudinal and many crossveins yellow with dark brown margins, or reddish to dark brown; veinlets and crossveins yellow and/or brown. Rs with at least two, but sometimes three or four clear forks. Ambient vein and axillary cord setae brown. *Forewing*. Costal area not expanded in basal part of wing, essentially parallel from near base to pterostigma. Pterostigma very poorly developed, comprising two to five veinlets, opaque membrane pigment absent or occupying portions of one to four cells, cream or pale yellowish. Apical area containing three to five branched and unbranched veinlets, with ca. ten to twenty one crossveins. Sc space with eight to fifteen crossveins in distal half. Five to seven presectoral crossveins. Cubital triangle with five to seven prefork crossveins; distal domain comprising two to four irregular cells, apical cell distally truncate, broad. One or two triangular marginal cells present, sometimes connected to cubital triangle by a crossvein. Cup+1A anastomosis position approximately halfway between origin and Cu fork. 3A well-developed, fusing with 2A a short distance before separating and continuing to posterior wing margin at axillary angle. Anal area with four to six irregular veinlets and two to three crossveins. Anal angle ca. 45 degrees of wing axis, evenly curved. Posterior wing margin distad of angle somewhat narrow, concave at and then expanding distad of Cup+1A. *FW maculation*. Margination conspicuous on many perpendicular veinlets subtending R, within mediocubital area and cubital triangle, and often throughout wing posterad of R until ceasing conspicuously in posterior third of wing; marginations and membrane darkening of several cells forming an irregular linear series of maculae from basimesal portion of cubital area to posterodistal margin of apical area; in melanistic males, pigment occurs in identical areas of wings, but margining is more prevalent and thicker such that many cells are completely pigmented. Male apical pigment patch (A1 Fig. 70) somewhat variable in its density and coverage, generally covering pterostigma and most of apical area except for posterior-most portion, distal portions of post-sectoral area and radial area, including anterior portions of compressed domain of subapical field. *Hind wing*. Costal area not expanded in basal part of wing, essentially parallel from near base to pterostigma. Pterostigma very poorly developed, comprising two to five veinlets, opaque membrane pigment absent or occupying portions of one to four cells, cream or pale yellowish. Apical area containing three to four branched and unbranched veinlets, with twelve to seventeen crossveins. Sc space with three to fourteen crossveins in distal half. Four to six presectoral crossveins. Medial triangle with five to seven pre-fork crossveins; distal domain comprising two to three cells. Two to three triangular marginal cells present. Posterior wing margin convex in anal area, broadly concave posterad of Mp_2 fork, becoming weakly convex through posterior medial area, and then subparallel to anterior margin until wing apex. *HW maculation*. Margination often on many perpendicular veinlets subtending R; marginations and membrane darkening of several cells sometimes forming a very small macula in basimesal portion of posterior medial area, and usually forming a large macula in post-sectoral area, another elongate one in distal portion of radial area, and one in middle of apical area.

Abdomen. Shape and size of sexes similar, female slightly more robust. Surfaces of T2+T3 and S3 diverging distad; T4/S4 and T7/S7 more-or-less parallel; T5–T6 and S5–S6 converging. Segments brown to dark brown, often with pale brown distal margins; T1–T3 and S1–S3 sometimes extensively pale brown or yellowish. S2 and S3 bearing a sparse coat of long, very slender, brown setae; acrotergite 2 without dorsal setae.

Ectoprocts brown and orange. *Sexually dimorphic characteristics*. *Males*. T2 and T3 bearing a somewhat dense coat of long, very slender, white setae. Pulvini not protruding. *Females*. T2 and T3 bearing a sparse coat of long, very slender, white setae. T9 dark brown and orange.

Male terminalia (A1 Figs. 71, 72). 9th sternite posterior margin projecting forward slightly, subacute. Gonarcus dorsum arched in lateral view. Paramere stem darkened almost to base but not broadened, blades projecting beyond pelta two-fifths to one fourth length of gonarcus, apicoventral margins recurved toward stem, not splayed laterad in distal view. Pelta narrow almond-shaped, ventrally acuminate, mesal pores minute. Pulvini short, slightly shorter than width at base, bases broad and nearly touching, all surfaces bearing numerous medium-long, stiff, slender black setae. Gonosaccal membrane between pulvini very narrow, membrane bearing long, stiff, slender black setae. Hypandrium internum weakly sclerotized, ringlike.

Female terminalia (A1 Figs. 73, 74). Distivalvae small, globose, fused mesally, with little space between them, setae on ventral surfaces long and thick. Membrane between para-linguellar folds and T8 plates with setae rather sparse. Linguella dorsal bulb large, round, ventral sagittal ridge of tissue undeveloped. Interdens slightly larger, as wide as long, slightly flexed sagittally, with a thin ventral sagittal carina, apex bilobed. Ventrovalvae medium in size, somewhat shallowly invaginated dorsally, mesal surface setae short, black, and very robust.

Variation. Some melanistic males have pigment in the costal and subcostal area.

Natural history and immature stages.—In the 1920s a group of colleagues of the Royal Entomological Society of London exchanged a series of communications about a handful of unidentified ascalaphid larvae collected over several years in northern Malawi ("Karonga, Nyasaland") and Kenya (Poulton 1923, 1928; Withycombe 1923; van Someren 1924). Imagos were ultimately successfully reared from specimens collected from Nairobi and were compared by D. E. Kimmins to material in the British Museum, who concluded they were *A. kolbei* (Poulton 1928). That identification is consistent with distribution data assembled in this paper, which demonstrate that only *A. kolbei* has thus far been recorded from both Kenya and northern Malawi (A1 Fig. 121; although *A. intractabilis* and *A. lefebvrei* have been recorded from as nearby as Uganda—A1 Figs. 120 and 121). *Allocormodes kolbei* and *A. junodi* have both been recorded from southern Malawi, but only very few specimens of *A. junodi* are known (only two were available for this study). Thus the extent of the latter's geographic distribution is not yet certain. Adults of *A. junodi* and *A. kolbei* are distinct in size, wing shape, and wing patterning, suggesting that Kimmins's identification was correct and the larvae collected in Kenya were in fact *A. kolbei*. The two larvae reported from northern Malawi were presumed to be conspecific, but were apparently not identical, although actual differences between the specimens were not provided (Withycombe 1923). They may represent *A. junodi*, *A. kolbei* or both.

From the above-cited papers, the following larval habitat information can be extracted. The *Allocormodes* larvae were collected on several substrates. Two larvae from Malawi were collected from the bark of “Cedra rubber tree” in November of 1919 (Withycombe 1923). This is a common name of the species *Manihot glaziovii* (Alexander 1907) (Euphorbiaceae), a non-native cassava that has been planted extensively throughout parts of east Africa for rubber production. Although this plant has peeling, dark reddish brown papery bark (which might be suitable for hiding under), Poulton (1923) clarified that the larvae were actually collected from lichen on the tree. Two third-instar larvae from Kenya (Nairobi), which appeared “allied to” the ones from Malawi (Poulton 1923), were collected, respectively, on a wild lichen-covered fig tree and a post bearing dull and powdery decomposed green paint, and both larvae “greatly resembled their immediate surroundings” (Poulton 1923; van Someren 1924). A fifth larva, a second instar from Nairobi, was collected on the trunk of a *Dracaena* sp. (Asparagaceae) tree and also resembled its “blotchy” substrate (van Someren 1924). A sixth larvae, from Kenya, a presumed first instar, was collected from a coat sleeve and was thought to have fallen there from a tree (van Someren 1924). All of these reports (except the last) seem to indicate a preference of the larvae for cortical lichens or lichen-like substrates.

Withycombe (1923) described the morphology of the larvae as being highly cryptic and strongly resembling the coloring and texture of lichens. The scoli were well-developed, flattened, and capable of being adpressed to the substrate. This is the condition in *Ascalobyas* (Henry 1978a) and *Haploglenius* (Ardila Camacho and Jones 2012), which also appear to be cortical. The bodies of the Withycombe larvae, whose color was brown, were covered with black and white dolichasters. These dolichasters were highly specialized and diverse, intergrading from elongate trumpets to flattened scales, all with serrate distal margins (Withycombe 1923). Van Someren (1924) redescribed the same larvae, again describing them as having dark bodies and white scale-like setae, and questioned if they weren't *Tmesibasis* (see also Henry 1976). Later in the same paper, however, he clarified that he thought the genus might instead be *Allocormodes*, based on the abdominal coloring of the malformed reared imagos. Confirmed *Tmesibasis* larvae are unknown.

Van Someren (1924) reported on the feeding habits and preferences of the larvae collected in Nairobi, and that were discussed by Poulton (1923). These larvae made no effort to pursue prey, but only attacked prey that walked over them from in front or behind. The jaws were rapidly thrown up and back to close upon a passing prey item. Prey items were dropped as soon as they were sucked dry. Accepted prey included nine species of flies in seven genera and five families (Stratiomyidae, Calliphoridae, Muscidae, Sarcophagidae, Anthomyidae), a grasshopper (Acrididae), a cricket (Gryllidae), a cockroach (Blattidae), and two smooth-skinned lepidopteran larvae (Papilionidae, Hesperidae). Rejected prey included those from recognized distasteful groups (Meloidae, Pentatomidae, Fulgoridae), spiny or hairy lepidopteran caterpillars (Nymphalidae, Lymantridae, Lycaenidae), aphids, and curiously, an antlion adult and larvae (though it is not clear if any of these would be a natural prey item). Larvae ceased to feed several days before pupation.

Withycombe (1923) observed the Malawi larvae to expel a small drop of fluid from the tip of each jaw when chloroform was introduced to the box containing them, and he presumed this fluid to be a poisonous digestive ‘saliva’ (salivary excretion), as has been reported in some other neuropteran larvae. Van Someren (1924) later questioned whether or not it was used to kill prey. The existence of an immobilizing salivary venom has been confirmed for the larvae of *Ululodes mexicanus* (Henry 1977).

Cocoon formation and eclosion were observed inside glass-topped rearing boxes (van Someren 1924). The larvae were equipped with a three mm spinneret that was manipulated by moving the entire body. Using this organ, they initiated cocoon formation by first spinning a base, then stretched loose lines of silk from this base in a side-to-side manner across a chosen space. Once the network was complete, a sphere of silk smaller than the prone larvae was spun inside, with the flexed larvae crawling around inside the sphere. Cocoon creation took from 24 to 48 hours. The pupal stage lasted from five to six weeks, and terminated when the pupa chewed its way out of the cocoon. The imago subsequently emerged from the pupa.

Evidence that, in the natural environment, this species pupates in crevices of tree bark, was revealed during a visit by the author to The Natural History Museum (BMNH). There, a collection (presumably prepared by Kimmins) of some of the immature life stages of *Allocormodes* (putatively *A. kolbei*, based on locality) was discovered. Most notable among the pieces were two sections of bark of an unknown tree in which pupal cocoons were lodged. One of these pieces of bark, as well as several other immature specimens (1 egg, 1 first instar, 2 third instars—see A1 Excel file 1) from the Natural History Museum (BMNH), were borrowed for this study, but based on label data associated with the specimens it is not clear if any of them represent the exact specimen mentioned in the papers cited above. Probably, though, they were reared during the same time period of the cited studies.

Label data indicate that one adult specimen of *A. kolbei* (JRJ_01187—BMNH, examined) was collected at a UV light.

Primary types.—

Allocormodes kolbei van der Weele, 1909.

—Lectotype by present designation, ♂, MFNB, examined (not photographed). *Type locality*: Tanzania, Zanzibar (island), Mahonda (city) [-6.008427°, 39.240148°], 610 masl. *Label data*: "D. Ost-Afrika Mhonda Stichel V /// Mus. Berol. /// Syn-Type /// Lectotypus ♂ Allocormodes kolbei Weele design. Bo Tjeder 1973 /// Allocormodes Kolbei VdW Type /// kolbei N19/6 /// LECTOTYPE Allocormodes kolbei Jones ♂ design. J. R. Jones 2013 /// JRJ_01227". *Condition*: excellent; antennae and wings spread; no parts missing; terminus of abdomen removed at 7th segment, cleared and mounted on a small clear plastic card on specimen pin.

—Paralectotype ♀, MFNB, examined (not photographed). *Label data*: "Ost.Afrika /// Mus. Berol. /// Syn-Type /// Allocormodes Kolbei VdW Type /// 1254 /// kolbei N 19/6

/// nach Kolbe, 1897 (Neuropt. row D. Ost-Afrika): Ost-Afrika, ?Usambara, Dr. C.-W. Schmidt /// PARALECTOTYPE Allocormodes kolbei Jones ♀ design. J. R. Jones 2013 /// JRJ_01230". *Condition*: good, spread, dermestid holes in head, thorax and abdomen, right hind wing tip broken.

—Paralectotype ♂, MNHN, examined (not photographed). *Label data*: "MUSEUM PARIS AFRIQUE ORIENT. ANGL Simba Maurice de Rothschild 1906 /// TYPE /// Allocormodes kolbei vdWeele par type ♂ vdWeele /// JRJ_01213". *Condition*: excellent: right FW tip dinged, no parts missing.

At the end of van der Weele's original description he discussed the material he examined, a male and a female from the Berlin Museum and another male from the collection of Baron M. De Rothschild. He made no holotype designation, although he did use the word 'type' in his description. Throughout van der Weele's work he makes liberal use of the term type, sometimes applying it specifically to known specimens, and other times using it in a more abstract descriptive sense, but not always differentiating clearly between the two usages. For example, he did somewhat obliquely refer to the Berlin male as "typus" when discussing the De Rothschild male, which, he pointed out, expresses a few differences (it is melanistic, consistent with *A. woodi* Esben-Petersen); he also called the female "Kolbe's type". On the det labels of each of the two MFNB specimens van der Weele inscribed the word "type"; on the MNHN specimen, his determination label reads "par type". Tjeder (1992) included a dark red "lectotypus" label on the male MFNB specimen as part of his attempted revision of the genus (see

‘Introduction’, above). The MFNB male is here selected as lectotype, rendering the MFNB female and the MNHN male specimens as paralectotypes (Art. 74).

Allocormodes woodi Esben Petersen, 1927.

—Holotype ♂ [not ♀!], BMNH (A1 Fig. 68). *Type locality*: Malawi (no further information available). No JRJ database number affixed. *Condition*: moderate, spread, antennae missing, right FW and left HW tips missing.

The *A. woodi* holotype specimen was examined briefly and photographed during a visit to The Natural History Museum (BMNH), but not borrowed on loan for further examination. Esben-Petersen (1927) indicated that the holotype specimen was a female, but it is clearly a male on the following accounts: (i) wings melanistic, characteristically darkened; (ii) white pigment patch on the left forewing present. All melanistic individuals examined in this study of this and the other species were males.

Additional material examined.—*Democratic Republic of the Congo*: 1 female [RMCA: JRJ_01193]. *Kenya*: 4 males, 5 females [BMNH: 3 males, 2 females, JRJ_00030 (A1 Fig. 65), JRJ_01203, JRJ_00049 (A1 Fig. 66), JRJ_00032, JRJ_01204; CAS: 1 male, 3 females, JRJ_00048, JRJ_00031, JRJ_00033, JRJ_00034]. *Malawi*: 1 male [BMNH: JRJ_01206]. *Tanzania*: 1 male, 2 females [BMNH: JRJ_01188, JRJ_01187 (A1 Fig. 67); MFNB: 1 female, JRJ_01229]. *Locality uncertain*: 1 male, 1 female [MFNB: JRJ_00050, JRJ_01228].

Discussion.—Melanistic males of *A. kolbei* (= *A. woodi*; A1 Figs. 66, 68) are quite peculiar in appearance, and it is easy to see why Esben-Petersen (1927) could consider them a unique species. Their dark wings set them apart from nearly all other *Allocormodes* species (*A. nigris*, newly described here, also has melanistic males). Nevertheless, except for wing pigment, they agree in all aspects of adult anatomy (including genitalia) with non-melanistic *A. kolbei*. Further, there is broad overlap in the geographic distributions of melanistic and non-melanistic specimens (A1 Fig. 121). Together, these morphological and distribution data support the placement of *woodi* as a new synonym of *A. kolbei*.

Allocormodes lefebvrei *van der Weele*

(A1 Figs. 23, 75–82, 121)

Allocormodes lefebvrei van der Weele

—van der Weele 1909.01.05 r#420: 74, fig. 43 {OD: ♂, DIS, ET. TS: not indicated [syntypes: 2 ♂♂; a lectotype needs to be designated from syntype material]. TL: “Französisch-Congo”. TR: MNHN, VDWC. Syntypes not examined (see “Primary types”, below).}

—Soldanski, H. 1912 r#5787: 120, fig. 2 {DIS, GD, RD: ♂♀, SR, SYN, TS}

Etymology and nomenclatural notes.—*lefebvrei*: a Latinized noun in the genitive case (Art. 11.9.1.3), named by van der Weele (1909) for the French ascalaphid systematist Alexandre Louis Lefèbvre.

Diagnosis.—Width of costal area of hind wings even throughout length; HW medial fork inside angle approximately 90 degrees; post-fork portion of medial triangle short, comprising 1 cell; in males, antennae greater than four-fifths forewing length, reaching nearly to pterostigma; overall size large.

Proposed autapomorphies.—Average antennae length to forewing length ratio of males long, ≥ 0.83; wings proximate in length, with average hind wing length to forewing length ratio of males ≥ 0.92; HW medial triangle distal domain short.

Distribution (A1 Fig. 121).—Sub-Saharan tropical belt: Cameroon, Equatorial Guinea, Uganda. In addition to the localities documented from material examined, van der Weele (1909: 75) mentions two specimens from “French Congo” (=Gabon).

Description.—

Size (mm). Male: body length 26 (25–26), abdomen 14 (13–16), forewing 43 (40–44), hind wing 37 (37–41), antennae 36 (34–38). Female: body length 28 (26–29), abdomen 17 (16–17), forewing 48 (47–48), hind wing 45 (44–45), antennae 35 (33–36).

Head. Occiput dull to glossy, dull yellow to brown. Postorbital sclerite dull yellow to brown. Vertex pattern variable, yellow plates not elevated above dark regions. Anterior extra-torular sclerites amber brown, only slightly lighter than frons. Frons brown, sometimes slightly yellowish, setae brown. Clypeus yellowish to brown, setae brown. Paraocular band brown. Anterior tentorial pit open ventrally as a round pit. Posterior genal triangle brown. *Mouthparts*. Labrum brown, setae dark brown and golden brown. Mandibles dull brown basally, reddish brown subapically, apices dark brown. Maxillary stipes and palpomeres brown, stipes and palpomere 1 setae brown. Labium: submentum and mentum setae dull yellow; labial palpi brown; ligula dull amber brown. *Eyes.* Golden brown. *Antennae.* Scape yellowish to brown, setae brown and white. Pedicel brown with an orange brown distal margin. Flagellum with 30-31 flagellomeres, base color dull yellow to reddish brown, with a narrow dark and then pale ring at each flagellomere node, often only darker ring expressed distally, setitori present, dark brown, giving flagellomeres a dark appearance, more dense proximal to club. Club narrower and slightly more elongate than in other species, with 6–8 flagellomeres, dull yellow to dark reddish brown formed by pigment spot at base of each short black seta, very slightly paler ventrally.

Thorax (A1 Fig. 77). *Cervix*. Dorsal cervical plates orangish laterally, otherwise brown to dark brown, setae brown. Cervical sclerite brown, anterior subapical setae brown. Ventral cervical plate knob round, very pale brownish yellow, setae pale yellow. *Pronotum*. Setae somewhat numerous, long, wispy, brown. Prescutum sulcus brown or sometimes narrowly orangish, lobes dark brown, yellow orangish laterally. Scutum dorsally brown, sublateral area sometimes with diffuse small orangish yellowish maculae, posterolateral knob dark brown. Scutellum very dark brown dorsally, orangish yellow laterally, bearing numerous long, very slender, brown setae laterally, pale yellow posteriorly. *Mesonotum*. Prescutum lobes brown, anteriorly orangish, entire surface bearing long, very slender, brown setae. Scutum very dark brown, pattern of orangish maculations weakly expressed and diffuse, all surfaces bearing, very slender, brown setae. Scutellum brown, orangish posterolaterally, posterior swelling divided by a short yellow longitudinal stripe or macula, surfaces bearing long, very slender, brown setae, more dense posteriorly. Subscutellum dull brown. Postnotum dark brown, laterally orangish. *Metanotum*. Paraprescutum brown. Prescutum brown, glabrous. Scutum brown, microtrichia slightly golden brown, lateroposterior margins bearing long, very slender, brown setae. Scutellum brown, posterior swelling sometimes with small medial orangish macula and laterally orangish, surfaces bearing long, very slender, brown setae. *Pleuron*. Pleurites mostly brown, but with some diffuse dull yellowish patches of varying size on various pleurites, all pleural surfaces bearing a sparse coat of long, very slender, dull yellowish or pale brown setae.

Legs. Coxal setae dull yellowish or pale brown. Femora and tibia evenly dull yellowish to reddish brown, dorsal surface of tibia one third distance from origin with thin transverse reddish or brown pigment line, space from line to origin sometime darkened reddish brown, spurs reddish brown; setae as follow: *prothoracic leg setae*: FD: long, very slender, white; FV: short slender stiff black; FAL: short slender stiff black; FPL: long, very slender, white; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow except at proximal and distal margins of patch where they are black; TPL: long thin stiff black; *mesothoracic leg setae*: FD: distally, sparse medium long stiff black; FV: medium and long stiff black mixed with long dull yellowish; FAL: very short stiff black proximally mixed with medium long, very slender, dull yellow; FPL: medium and long stiff black mixed with long dull yellowish; TD: mixed short and medium stiff slender black; TV: mixed short and medium long slender black; TAL: mixed short and medium stiff slender black; TPL: mixed short and medium long slender black; *metathoracic leg setae*: as on mesothoracic leg. *Tarsi*. Dull yellowish to reddish brown but sometimes slightly more reddish.

Wings (A1 Figs. 23, 75, 77, 78). Major longitudinal and many crossveins dark brown, Sc+R disted of anastomosis yellow; veinlets and crossveins yellow and/or brown. Rs with at least two, but sometimes three or four clear forks. Ambient vein and axillary cord setae brown. *Forewing*. Costal area not expanded in basal part of wing, essentially parallel from near base to pterostigma. Pterostigma in males essentially obliterate, barely visible as a cream tint over two to three cells against opaque white background of apical patch; in females, brownish translucent pigment traversing two to four cells proximally, distad of these one to three additional cells with hint of opaque cream pigment flecked with minute brown granules in center of membrane. Apical area containing six to ten branched and unbranched veinlets, with ca. seven to fifteen crossveins. Sc space, in males, with six to twelve veinlets in distal half; in females, with thirteen to nineteen veinlets in distal half. Four to eight presectoral crossveins, sometimes irregular near Rs. Cubital triangle with five to seven prefork crossveins; distal domain comprising one to two irregular cells, apical cell distally truncate. One or two triangular marginal cells present, second cell often connected to cubital triangle by a crossvein. Cup+1A anastomosis position variable, more-or-less halfway between origin and Cu fork. 2A+3A well-developed, diverging soon after convergence into an irregular network of oblique veinlets and crossveins. Anal area with several oblique veinlets and crossveins. Anal angle evenly and sharply curved, subacute. Posterior wing margin distad of angle narrow, concave at and then expanding distad of Cup+1A. *FW maculation*. Margination conspicuous on many perpendicular veinlets subtending R, in cubital area along posterior wing margin immediately distad of cubital triangle, in post-sectoral and mediocubital areas where Mp_1 curves strongly toward posterior wing margin, and often throughout wing posterad of R. Male apical pigment patch (A1 Fig. 78) covering wing apex from pterostigma posterad and apicad, covering apical area except for posterior-most portion, and radial area (including compressed domain of subapical field) except for distal portions. *Hind wing*. Costal area not expanded in basal part of wing, essentially parallel from near base to pterostigma. Pterostigma very poorly developed, diffuse brown pigment and occasionally also opaque cream pigment in five to six cells comprising four to five veinlets. Apical area. Sc space, in males, with six to twelve veinlets in distal half; in females, with thirteen to nineteen veinlets in distal half. Three to seven presectoral crossveins. Medial triangle with six to nine pre-fork crossveins; distal domain comprising two cells. One to two triangular marginal cells present. Posterior wing margin convex in anal area, broadly concave posterad of Mp_2 fork, becoming broadly convex through posterior medial area, and then subparallel to anterior margin until wing apex. *HW maculation*. Margination on many perpendicular veinlets subtending R; marginations and membrane darkening of several cells forming a macula in post-sectoral area and anterior medial space at curve of Mp_1 near posterior wing margin, in radial area near posterior wing margin in radial area posterad of Sc-R anastamosis, and in posterior portion of apical area.

Abdomen. Shape and size of sexes similar, female more robust. Surfaces of T2+T3 and S3 diverging, of T4/S4 to T6/S6 converging distad. Surfaces of T7/S7 more-or-less parallel. Segments cinnamon to dark brown, sometimes with slightly paler distal margins; T1–T3 and S1–S3 sometimes with irregular diffuse yellowish maculations. T1, T2 and corresponding pleural membrane with a sparse coat of long, very slender, brown setae; S2 with a dense coat of long, very slender, pale yellow setae. Ectoprocts brown with diffuse dull orange markings. *Sexually dimorphic characteristics*. *Males*. Proximal half of S3 with a sparse coat of long, very slender, pale yellow setae. Pulvini protrusion uncertain. *Females*. T9 brown with diffuse dull orange markings.

Male terminalia (A1 Figs. 79, 80). 9th sternite posterior margin not projecting forward, nearly square. Gonarcus dorsum weakly arched in lateral view. Paramere stem short, broad, not reaching to base of gonarcus, distal blades projecting beyond pelta one-fifth length of gonarcus, apicoventral margins slightly projecting ventrad of paramere stem but not recurving, only slightly splayed laterad in distal view. Pelta almond-shaped, ventrally acuminate, mesal pores minute. Pulvini narrow, two to three times longer than width at base, bearing medium-long, stiff, slender brown setae, mesal surfaces glabrous.

Gonosaccal membrane between pulvini with some setae. Hypandrium internum a small sclerotized cone.

Female terminalia (A1 Figs. 81, 82). Distivalvae medium small, globose, fused mesally, with little space between them, setae on ventral surfaces medium long. Membrane between para-linguellar folds and T8 plates with setae rather sparse. Linguella dorsal bulb moderately large, ventral sagittal ridge of tissue slightly developed, somewhat broad. Interdens very small, weakly developed, weakly sclerotized, longer than wide, tab-shaped. Ventrovalvae medium small, somewhat shallowly invaginated dorsally, mesal surface setae short, brown.

Variation. There is some slight variation in the lengths of the antennae (see A1 Excel file 2).

Natural history and immature stages.—Unknown.

Primary types.—

Allocormodes lefebvrei van der Weele, 1909

—Syntype ♂, MNHN, not examined. *Label data*: van der Weele indicated it originated from “Französisch-Congo” (Gabon). *Condition*: abdomen ‘destroyed’ (van der Weele 1909).

—Syntype ♂, VDWC, not examined. *Label data*: van der Weele gave it as ‘N., Gomo, Ogoué, H. Ellenberger’ (=Gabon). *Condition*: unknown.

Van der Weele described *A. lefebvrei* from two specimens. The MNHN specimen was not found during a visit to the Paris Museum. The current repository of the second specimen, which van der Weele indicated was in his private collection, is unknown.

Additional material examined.—*Cameroon*: 1 male, 1 female [CMNH: JRJ_00035 (A1 Fig. 75), JRJ_00037 (A1 Fig. 76)]. *Equatorial Guinea*: 1 male, 1 female [MFNB: JRJ_01231, JRJ_00038]. *Uganda*: 1 male [BMNH: JRJ_00036].

Discussion.—This is one of the largest and most conspicuous species of *Allocormodes*. It is closely related to *A. kolbei*, which it strongly resembles in wing shape, apical pigment patch shape, and antennae morphology, but the two differ in size, thorax coloring, wing maculation, and geographic distribution. The female is newly described here.

Allocormodes maculipennis *(Taschenberg)*

(A1 Figs. 83–91, 122)

Haploglenius maculipennis Taschenberg

—Taschenberg 1879 r#5954: 218 {OD: ♂, DIS. TS: not indicated [holotype]. TL: "Eliva Jonango (Westen Mittelafrikas)". TR: ZMH. Holotype not examined (see "Primary type", below).}

—Gerstaecker 1894 r#2559: 100 {JSYN (of *Ascalaphus intractabilis* Walker)}

Allocormodes maculipennis (Taschenberg)

—van der Weele 1909.01.05 r#420: 72, fig. 41 {GD, RD: ♂♀, SYN, TS, TR}

—Soldanski, H. 1912 r#5787: 120, fig. 1{DIS, GD, RD: ♂♀, SR, SYN, TS, TR}

—Navás 1925 r#795: 123 {SR}

Etymology and nomenclatural notes.—from *macula* (Latin), 'spot, stain, mark'; *penna*, *pinna* (Latin) 'feather, wing', ='maculated wing'; noun in apposition. Taschenberg provides no explicit explanation for the name given, but his description includes numerous details about the distribution of maculation on the wings, and presumably it indicates the conspicuous wing patterning.

Diagnosis.—Triplet of cubital area margined veins in forewing. Hind wing pterostigma cream and dark brown. Cervical sclerite yellow.

Proposed autapomorphies.—Mesoscutal velvety spots large; triplet of margined veins in cubital area.

Distribution (A1 Fig. 122).—Sub-Saharan tropical belt: Sierra Leone, Gabon, Equatorial Guinea, Ghana, Cameroon, Nigeria, Uganda. The lack of material from Congo and the Democratic Republic of the Congo is likely an artifact of insufficient collecting in the area.

Description.—

Size (mm). Male: body length 29 (28–30), abdomen 19 (17–20), forewing 38 (37–38), hind wing 32 (31–33), antennae 25 (24–25). Female: body length 29 (27–30), abdomen 17 (16–19), forewing 41 (40–43), hind wing 36 (35–39), antennae 24 (21–25).

Head. Occiput glossy, dark reddish brown and pale yellow. Postorbital sclerite pale to dark yellowish or brown. Vertex pattern slightly asymmetrical from side to side, lateral plates large, yellow, dark regions not completely dark, but rather yellowish or reddish and blending with yellow plates dorsally, bearing long, very slender, dark brown setae. Anterior extra-torular sclerites pale to dull yellow. Frons amber to dark reddish brown, setae dark brown. Clypeus amber to dark reddish brown, setae dark brown. Paraocular band dark reddish brown along eye, paler yellowish brown ventrad near mandible base and along tentorial pit. Anterior tentorial pit closed. Posterior genal triangle pale to reddish brown. *Mouthparts*. Labrum dark reddish brown, setae dark brown. Mandibles orangish to dark brown basally, bearing medium length thin dark brown setae, apices very dark brown. Maxillary stipes yellowish, palpomeres reddish brown, stipes and palpomere 1 setae dark brown. Labium: submentum and mentum yellow to dark reddish brown, setae dark brown; labial palpi reddish brown; ligula reddish brown. *Eyes.* Golden brown. *Antennae.* Scape dark reddish brown, sometimes yellow anteromesally, setae dark brown. Pedicel reddish brown. Flagellum with 26–28 flagellomeres, yellow to medium brown, pigment darker at flagellomere nodes, darkening closer to club, darkened setitori weakly expressed close to club. Club with 11 flagellomeres, base color yellowish but club appearing dark brown dorsally from high concentration of pigment spots at base of numerous short black seta, yellow ventrally where spots not expressed.

Thorax (A1 Fig. 86). *Cervix*. Dorsal cervical plates dark brown mesally, orange laterally, setae brown. Cervical sclerite pale yellow to orangish, anterior subapical setae dark brown. Ventral cervical plate knob ovoid, pale yellow to brown, setae brown. *Pronotum*. Setae long, wispy, dark brown. Prescutum yellow laterally and along median sulcus, with broad, dark brown parasagittal macula. Scutum dark brown, narrowly yellow along sagittal line, broadly yellow sublaterally, posterolateral knob dark brown. Scutellum dark brown dorsally, sulcus lined with a narrow yellow stripe, yellow anterolaterally, bearing numerous long, very slender, dark brown setae. *Mesonotum*. Prescutum lobes dark brown, with a round yellow spot on posterior surface and another on lateral surface of each lobe, entire surface bearing long, very slender, dark brown setae. Scutum dark brown with numerous yellow maculae, yellow patterning somewhat variably expressed, sometimes very weakly: yellow maculation laterally near wing base, surrounding velvety spot, sagitally, and a larger area posterad of velvety spot, this area divided longitudinally by a dark brown maculation, all surfaces bearing long, very slender, dark brown setae, except for distinct patch of golden yellow to white setae immediately posterad of velvety spots. Scutellum dark brown, yellow laterally, along posterior margin, and as a broad sagital stripe or macula on posterior transverse swelling, lateral and posterior surfaces bearing sparse, long thin, very slender, dark brown setae. Subscutellum yellow to brown. Postnotum brown, glabrous. *Metanotum*. Paraprescutum yellow to dull orange or brown, glabrous. Prescutum dark brown, sometimes with a tiny yellow median macula, entire surface bearing sparse long, very slender, brown setae. Scutum dark brown, sometimes with diffuse yellowish macula laterally, microtrichia cinnamon brown, posterolateral surfaces bearing long, very slender, dark brown setae. Scutellum dark brown, posterior and lateral margins paler, yellow to brown, dorsal surface bearing long, very slender, white setae, posterolateral surfaces with long, very slender, dark brown setae. *Pleuron*. Pleurites evenly brown to dark brown, bearing a moderately thick coat of long, very slender, dark brown setae.

Legs. Coxal setae dark brown. Femora medium brown to dark reddish brown; tibiae yellow to brown, with brown spots as bases of setae, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long stiff black; FV: short slender stiff black; FAL: short slender stiff black; FPL: long stiff black; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow; TPL: with long thin stiff black; *mesothoracic leg setae*: FD: long slender black; FV: stiff medium length black; FAL: short black; FPL: long stiff black; TD: sparse stiff medium length black; TV: long stiff black; TAL: medium short stiff black; TPL: medium short stiff black; *metathoracic leg setae*: FD: mixed very short stiff and very long slender black; FV: long slender stiff black; FAL: mixed medium short slender and stiff black; FPL: long slender stiff black; TD: short stiff black; TV: medium short stiff slender black; TAL: medium long stiff black; TPL: medium long stiff black. *Tarsi*. Reddish brown.

Wings (A1 Figs. 83–85, 87). Most veins, veinlets and crossveins brown to dark brown, a few veinlets and crossveins near wing base sometimes yellow. Rs with two unambiguous forks. Ambient vein and axillary cord setae brown. *Forewing*. Costal area slightly expanded in proximal third of wing, gradually narrowing such that C and Sc become approximately parallel past midpoint until, in males, diverging very slightly at pterostigma or, in females, remaining essentially parallel. Pterostigma comprising five to seven mostly unbranched veinlets, opaque cream-colored membrane more-or-less filling cells, proximal two to five cells suffused with brown to very dark reddish brown pigment. Apical area containing four to six branched and unbranched veinlets, with 14 to 25 crossveins. Sc space without crossveins. R subtending veinlets occasionally widely spaced. Four to six regular presectoral crossveins, rarely these connected by irregular crossveins. Cubital triangle with five prefork crossveins; distal domain comprising two to four irregular cells. A single triangular marginal cell present, sometimes connected by a crossvein. Cup+1A anastomosis usually two thirds distance from origin to Cu fork. 2A+3A very robust, diverging into several irregular forks in proximal half of anal area. Anal area with several oblique veinlets and crossveins. Anal angle ca. 45 degrees of wing axis, essentially straight. Posterior wing margin at cubital area marginal cell slightly concave, posterior wing margin slightly expanded and curving around cubital area, narrowing again at Mp_1 and again slightly at Rs_1, in females span in between Mp_1 and Rs_1 appearing drawn in. *FW maculation*. Many veinlets subtending R margined; veinlets and crossveins often margined in radial area immediately posterad of pterostigma, in post-sectoral area near wing margin, and in distal-most portion of cubital area near Mp_2+Cua and wing margin; aggregates of veinlets and crossveins margined to form small diffuse maculae in distal-most portion of apical area anterad of compressed domain of radial area of subapical field, in radial area proximad of compressed domain at wing margin, and in post-sectoral area at bend of Mp_1 near wing margin; a conspicuous margined triplet (but sometimes four or five) of oblique crossveins in the cubital area positioned in the fourth row of cells striking the wing margin distad of the cubital triangle; anal area crossveins margined; many other veinlets and crossveins throughout the wing often margined. Male apical pigment patch (A1 Fig. 87) covering wing apex from pterostigma apicad and posterad, covering apical and subapical fields, including compressed domain of subapical field, except for dark maculae. *Hind wing*. Costal area conspicuously expanded in proximal fourth of wing, then narrowing such that C and Sc become approximately parallel at midpoint until immediately preceding pterostigma, when area expands again very slightly. Pterostigma similar to as in FW, longer in males, variable (in one male pigment very dark), comprising five to seven mostly unbranched veinlets, opaque cream-colored membrane more-or-less filling cells, proximal two to five cells suffused with brown to very dark reddish brown pigment. Apical area containing four to five branched and unbranched veinlets, with 9 to 26 crossveins, fewer in males. Sc space without crossveins. Three to four presectoral crossveins. Medial triangle with four to six pre-fork crossveins; distal domain comprising three to four cells. Usually two but sometimes three trapezoidal or triangular marginal cells present, these sometimes connected by a crossvein and rarely divided by another irregular crossvein. Posterior wing margin distad of anal angle convex, posterior margin slightly emarginate at Mp_1 and Rs_1, span in between Mp_1 and Rs_1 drawn in very slightly in females. *HW maculation*. Many veinlets subtending R often margined; veinlets and crossveins often margined in radial area immediately posterad of pterostigma and in distal-most portion of posterior medial area near Mp_{2a} and wing margin; aggregates of veinlets and crossveins margined to form small diffuse maculae in distal-most portion of apical area anterad of compressed domain of radial area of subapical field, in radial area proximad of compressed domain at wing margin, and in post-sectoral area at bend of Mp_1 near wing margin; sometimes one to several crossveins margined in posterior medial area near wing margin two or three cell rows distad of medial triangle; other veinlets and crossveins throughout the wing sometimes margined.

Abdomen. Outlines of T2+T3 and S3 diverging distad; outlines of T4–T6 and S4–S6 and sometimes segment 7 converging. Tergites and sternites dark brown with pale brown or yellow distal margins; in some specimens T1–T3 very pale brown or mottled yellow, sometime entirely yellowish. T1 bearing erect, very slender, brown setae. S2 and S3 bearing a somewhat sparse covering of long, very slender, brown setae. Ectoprocts dark brown. *Sexually dimorphic characteristics*. *Males*. T2 and proximal half of T3 bearing somewhat dense patch of golden brown or white, very slender, setae; pleural membrane of segments 2 and 3 bearing a thick coat of long, very slender, brown setae. Pulvini protrusion uncertain, but probably slight. *Females.* T2 and proximal half of T3 bearing sparse patch of golden brown or white, very slender, setae; pleural membrane of segment 2 bearing a sparse coat of long, very slender, brown setae. T9 dark brown with distal margins thinly pale brown, ventrodistal margin with small pale brown macula.

Male terminalia (A1 Figs. 88–89). 9th sternite posterior margin not projecting forward, nearly square. Gonarcus dorsum weakly arched in lateral view. Paramere stem not darkened, reaching base of gonarcus, blades projecting beyond pelta one-fourth length of gonarcus, apicoventral margins slightly projecting ventrad of paramere stem but not recurving, somewhat to widely splayed laterad in distal view. Pelta conspicuous, broadly almond-shaped, mesally depressed, ventrally blunt, mesal pores numerous. Pulvini narrow, approximately two times longer than width at base, widely separated, bearing medium-long, stiff, slender brown setae, mesally glabrous. Gonosaccal membrane between pulvini with some setae mesally. Hypandrium internum sclerotized ventrally, somewhat basketlike.

Female terminalia (A1 Figs. 90–91). Distivalvae small, oblong, fused mesally but clearly separated with space between them, setae long, thick, dark brown. Membrane between para-linguellar folds and T8 plates with setae dense, long, dark brown. Linguella dorsal bulb medium large, ovoid, with dark brown setae, ventral sagittal ridge of tissue developed. Interdens medium small, somewhat sclerotized, as wide as long, spoon- or wedge-shaped. Ventrovalvae medium large in size, somewhat shallowly invaginated dorsally, mesal surface setae short, dark brown, robust.

Variation. One male and one female from Nigeria (JRJ_01207) and Ghana (JRJ_00042), respectively, display extensive white setae on the pterothorax, but otherwise match other specimens of *A. maculipennis* nearly completely. In both specimens, the following features occur: *Mesonotum*: Scutellum: a few specimens with a dense mesal patch of short white setae and a posterior fringe of long white setae. *Metanotum*: Prescutum entire surface bearing sparse long, very slender, white setae. Scutum posterolateral surfaces bearing long, very slender, dark brown and/or white setae. Coxae with thick coat of long, very slender, white setae. Apical area possessing fewer crossveins, 13 to 20. The pteropleural setae of JRJ_00042 are brown near the wing bases but otherwise white; abdominal T1 also bears white and not brown setae.

In JRJ_00039, the forewing Cup+1A anastomosis position is almost at the Cu fork, and the costal veinlets are margined. In JRJ_00043 and JRJ_01210, the right FW marginal cell is absent. The HW pterostigma pigment is very thick and the dark portion dark in JRJ_00039.

Natural history and immature stages.—Most examined specimens of *A. maculipennis* were collected at elevations between 300 and 1200 meters (see A1 Excel file 1). The larvae are unknown.

Primary type.—

Haploglenius maculipennis Taschenberg

—Holotype ♂, ZMH, not examined. *Type locality*: Gabon, "Eliva Jonango" (lake). *Label data*: Based on comments in Taschenberg's original description and van der Weele (1909), probably: 'Eliva Jonango, Westen Mittelafrikas, v. Koppenfels'. *Condition*: unknown.

Van der Weele indicated that Taschengberg's type was 'incompletely developed' (teneral), having yellowish-brown wing venation and light brown wing maculation.

The exact location of “Eliva Jonango” is uncertain, but the name appears to represents a stretch of water along or near the Ogooue [“Ogobai”] River in Gabon, also, at one time, called Lake Jonanga (du Chaillu 1867: 103, 414).

Additional material examined.—*Cameroon*: 1 female [CIRAD: JRJ_00043 (A1 Fig. 84)]. *Equatorial Guinea*: 1 male [MFNB: JRJ_00039 (A1 Fig. 83)]. *Ghana*: 1 female [BMNH: JRJ_00042]. *Nigeria*: 1 male, 1 female [BMNH: 1 male , JRJ_01207; USNM: 1 female, JRJ_00044]. *Sierra Leone*: 1 female [BMNH: JRJ_01209]. *Uganda*: 1 female [BMNH: JRJ_01210].

Discussion.—In addition to Taschenberg’s type specimen, Van der Weele (1909) states that he examined a female from the Paris Museum, which he figured. The female was not discovered during a visit to the Paris Museum. The description here is based on a series of examined specimens that match van der Weele’s figure and description.

Allocormodes maynei *(Navás)*

(A1 Figs. 92–96, 122)

Allocormodes maynei Navás

—Navás 1925 r#795: 124 {OD: ♀, DIS, ET. TS: not indicated [holotype]. TL: “Bumputu”. TR: RMCA. Holotype examined (see “Primary types”, below).}

Etymology and nomenclatural notes.—*maynei*: a Latinized noun in the genitive case (Art. 11.9.1.3), named by Navás (1925) for R. Mayné, collector of the type specimen.

Diagnosis.—Less margining on veinlets and crossveins than in other species. Distinct blotches on wings (cells pigmented, not only veins); R1 veinlets widely dispersed. Hind wing pterostigma cream and dark brown. Cervical sclerite dark brown.

Proposed autapomorphies.—Setal spots present at base of most setae on flagellomere internodes in distal half of antennae; cervical sclerite apex brown; FW pigment maculation with edges coarse and sharp, contrasted with non-pigment membrane; HW pigment maculations non-linear, not strictly mesolongitudinal.

Distribution (A1 Fig. 122).—Central Africa: Democratic Republic of the Congo.

Description.—

Size (mm). Male: unknown. Female: body length 31 (est.), abdomen 17 (est.), forewing 41 (est.), hind wing 38 (est.), antennae 24 [body and wing lengths given here are estimates, as the abdomen is broken off and the wingtips are tattered and missing, and as such differ slightly from measurements given by Navás (1925)].

Head. Occiput glossy, brown and orange. Postorbital sclerite orangish. Vertex pattern asymmetrical from side to side, lateral plates large, orangish, dark regions bearing long, very slender, brown setae. Anterior extra-torular sclerites pale yellow. Frons brown, setae dark brown. Clypeus reddish brown, setae dark brown. Paraocular band brown, orange adjacent to clypeus. Anterior tentorial pit closed. Posterior genal triangle brown. *Mouthparts*. Labrum reddish brown, setae dark brown. Mandibles orangish brown basally, reddish brown subapically, apices dark brown. Maxillary stipes and palpomeres reddish brown, stipes and palpomere 1 setae dark brown. Labium: submentum and mentum setae dark brown; labial palpi reddish brown; ligula reddish brown. *Eyes*. Golden brown. *Antennae*. Scape dark reddish brown, setae dark brown. Pedicel reddish brown. Flagellum with 27 flagellomeres, yellowish brown, pigment darker at flagellomere nodes, darkening closer to club, darkened setitori weakly expressed. Club with 11 flagellomeres, base color yellowish but club appearing dark brown dorsally from high concentration of pigment spots at base of numerous short black seta, yellow ventrally.

Thorax (A1 Fig. 93). *Cervix*. Dorsal cervical plates dark brown, setae brown. Cervical sclerite dark brown, subapical surface setae dark brown. Ventral cervical plate knob ovoid, pale brown, setae brown. *Pronotum*. Setae somewhat numerous, long, wispy, dark brown. Prescutum orange, with parasagittal dark brown maculation. Scutum dark brown, with orange macula sublaterally and on midline, posterolateral knob dark brown. Scutellum dark brown dorsally, orangish laterally, bearing numerous long, very slender, brown setae. *Mesonotum*. Prescutum lobes dark brown, with a round yellow spot on posterior surface and another very diffuse one on anterolateral surface of each lobe, entire surface bearing long, very slender, dark brown setae. Scutum dark brown, velvety spots appearing somewhat diffuse due to oily matting of setae, all surfaces bearing long, very slender, dark brown setae, setae immediately posterad of velvety spots golden yellow. Scutellum dark brown, orange laterally, along posterior margin, and medially on posterior transverse swelling, lateral and posterior surfaces bearing sparse, medium long thin, very slender, dark brown setae. Subscutellum dull orange brown. Postnotum brown, glabrous. *Metanotum*. Paraprescutum dull orange, glabrous. Prescutum brown with diffuse transverse orange macula, bearing sparse long, very slender, erect dark brown setae. Scutum dark brown, microtrichia cinnamon brown, remaining surfaces bearing golden microtrichia, mesal surfaces bearing a patch of golden yellow setae, lateroposterior margins bearing long, very slender, dark brown setae. Scutellum dark brown, lateral and posterior margins orange, bearing long, very slender, dark brown setae. *Pleuron*. Pleurites evenly dark brown, bearing a moderately thick coat of long, very slender, dark brown setae.

Legs. Coxal setae dark brown. Femora dark reddish brown; tibia yellowish brown, spurs dark reddish brown; setae as follows: *prothoracic leg setae*: FD: long stiff black; FV: short slender stiff black; FAL: short slender stiff black; FPL: long stiff black; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow mesally, black around margins of patch; TPL: long thin stiff black; *mesothoracic leg setae*: FD: long slender black; FV: stiff medium length black; FAL: short black; FPL: long stiff black; TD: in distal part, stiff medium length black; TV: long stiff black; TAL: medium short stiff black; TPL: medium short stiff black; *metathoracic leg setae*: FD: proximally short stiff black distally long slender black; FV: long slender stiff black; FAL: medium short slender black; FPL: long slender stiff black; TD: medium long stiff black; TV: long stiff slender black; TAL: medium long stiff black; TPL: medium long stiff black. *Tarsi.* Reddish brown.

Wings (A1 Figs. 92, 94a). Major longitudinal and many crossveins dark brown and yellow; many veinlets and crossveins throughout yellow. Rs with three clear forks. Ambient vein and axillary cord setae dark brown. *Forewing*. Costal area somewhat expanded in proximal fourth of wing, gradually narrowing such that C and Sc become approximately parallel at midpoint until diverging slightly proximad of pterostigma. Pterostigma comprising four to five mostly unbranched veinlets, opaque cream-colored membrane essentially filling cells, proximal two cells suffused with very dark reddish brown pigment, this margining veinlets of subsequent two cells. Apical area containing five to six branched and unbranched veinlets, crossveins numerous. Sc space without crossveins. R subtending crossveins widely spaced. Seven irregular presectoral crossveins. Cubital triangle with five pre-fork crossveins, distal domain comprising three irregular cells. A single triangular or trapezoidal marginal cell present. Cup+1A anastomosis position two thirds distance from origin to Cu fork. 2A+3A very robust, diverging into several short forks that strike posterior wing margin near wing base. Anal area with several oblique veinlets and crossveins. Anal angle ca. 45 degrees of wing axis, essentially straight. Anal angle distad of angle slightly concave, posterior wing margin slightly expanded but straight along cubital area, narrowing again at Mp_1 and Rs_1, span in between Mp_1 and Rs_1 appearing drawn in. *FW maculation*. Veinlets subtending R, in medicubital area, and in anal area margined, those in anal area broadly;

marginations and membrane darkening of several cells forming a concentrated macula posterad of Sc-R anastomosis, in cubital area distad of cubital triangle apex, in region spanning post-sectoral, mediocubital, and cubital areas near apex of cubital area, and in subapical field basad of compressed domain. *Hind wing*. Costal area conspicuously expanded in proximal fourth of wing, then narrowing such that C and Sc become approximately parallel at midpoint until immediately preceding pterostigma, when area expands again very slightly. Pterostigma comprising five branched and unbranched veinlets, opaque cream-colored membrane visible in distal three cells, proximal two cells and margins or remaining two to three cells suffused with very dark brown pigment. Apical area mutilated. Sc space without crossveins. Four presectoral crossveins. Medial triangle with six pre-fork crossveins; distal domain with four cells. Two trapezoidal marginal cells present. Posterior wing margin distad of anal angle very slightly concave, posterior wing margin slightly expanded but straight along posterior medial area, narrowing again at Mp_1 and Rs_1, span in between Mp_1 and Rs_1 appearing very slightly drawn in. *HW maculation.* Marginations and membrane darkening of several cells forming a concentrated macula posterad of Sc-R anastomosis, in region spanning post-sectoral and anterior medial areas near apex of posterior medial area, in subapical field or radial area along posterior wing margin, and in distal portion of apical area.

Abdomen. Outlines of T2+T3 and S3 diverging distad, outlines of T4–T6 and S4–S6 converging. Tergites and sternites dark brown with pale brown distal margins. T2 and proximal half of T3 bearing a sparse covering of medium length erect pale golden setae; S2 and S3 bearing a sparse covering of long, very slender, brown setae; pleural membrane of segment 2 bearing a coat of long, very slender, brown setae. Ectoprocts dark brown. *Sex specific characters. Female.* T9 brown, pale brown dorsally, a pale brown macula on proximomesal margin.

Male terminalia. Unknown.

Female terminalia (A1 Figs. 95, 96). The genitalia match those of *A. maculipennis* in nearly every detail.

Variation. None observed.

Natural history and immature stages.—Unknown.

Primary types.—

Allocormodes maynei Navás

—Holotype ♀, RMCA, examined (A1 Fig. 92). *Type locality*: Democratic Republic of the Congo, Bomputu (town) [-0.367392°, 20.102831°], 337 masl. *Label data*: "MUSÉE DU CONGO Bomputu 11-I-1918. R. Mayné /// R. DÉT. I 1028 /// Allocormodes Lefebvrei ? Weele Navás S. J. det. /// Cotypus /// CO-TYPE /// Allocormodes maynei NAVÁS ♀ det. Bo Tjeder 1970 /// Lectotypus Allocormodes maynei NAVÁS design. Bo Tjeder 1970 /// 00702 P /// LECTOTYPE Allocormodes maynei Jones ♀ design. J. R. Jones 2013 /// JRJ_01190". *Condition*: fair; right antennae broken off, missing; abdomen glued to a separate card but reattached for photography, then apex removed and macerated; wingtips shredded, posterior wing margins dinged.

Although two labels on the type specimen designate it as a cotype, there is no information in the literature, or in the source collection, to indicate that Navás ever looked at more than a single specimen when he made his original description. Navás provided only a single set of measurements and a single locality, collection date and collector in his description. Only one specimen of this species was found in the RMCA collection, and no addional specimens were seen in any other collections visited (BMNH, MNHN, USNM) or in loan material sent. Thus the specimen is here considered as holotype (Tjeder also applied an unpublished lectotype label to the specimen).

Additional material examined.—None.

Discussion.—Navás (1925) apparently described this species from a single female specimen, and no other specimens are yet known. At the time he described it, the female of *A. lefebvrei* was unknown, and he speculated that *A. maynei* might be the female of *A. lefebvrei*, but ultimately concluded that it representated a novel species. That conclusion is confirmed here—the females of *A. lefebvrei*, which are first described here, strongly resemble the males, and differ in numerous respects from the holotype of *A. maynei*. The wing maculation alone, which has unique large, non-linear maculae, easily sets *A. maynei* apart from *A. lefebvrei*, although it cannot yet be certain that all specimens would express the pattern equally.

On the basis of female genitalia alone, *A. maynei* could be placed as a subspecies of *A. maculipennis*, with which it is very similar; however, the wing pattern of *A. maynei* is so unique, that when considered in conjunction with other features that differ from *A. maculipennis* (cervical sclerite color, medial triangle distal domain length, distribution, etc.), recognition at species level seems best at present. Too few specimens of either species, but especially *A. maynei*, are yet known (and no males of *A. maynei* are yet known) to make a confident judgment. In the absence of more extensive population data, it is concluded that creation of a subspecies is undesirable.

Allocormodes micheli *n. sp.*

(A1 Figs. 97–104, 121)

[*Allocormodes maculipennis* (Taschenberg)]

—Michel 2000 r#9409: 53 {GD}

—Michel and Cadet 2009 r#13165 {FP, GD}

Etymology and nomenclatural notes.—*micheli*: a Latinized noun in the genitive case (Art. 11.9.1.3), named for Dr. Bruno Michel, a talented and distinguished French neuropterologist who has done much notable work on owlflies, particularly in West Africa, and who provided a series of specimens from there to make possible this description.

Diagnosis.—Short white setae patches on mesoscutum and metascutum behind velvety spots, posteriorly on mesoscutellum, laterally on metascutellum, and on T1, T2, and anterior half of T3; mesoscutellum mesal setae dark; small overall relative size, dark body color; distribution: West Africa (Burkina Faso, Mali, Nigeria).

Proposed autapomorphies.—Mesoscutellum posterior margin white setae fringe dense, setae short; outline of HW margin posterad of marginal cell(s), in males, concave; outline of pelta ventral margin acuminate.

Distribution (A1 Fig. 121).—West Africa: Burkina Faso, Mali, Nigeria.

Description.—

Size (mm). Male: body length 24 (23–27), abdomen 13 (12–15), forewing 31 (30–32), hind wing 27 (26–28), antennae 21 (20–22). Female: body length 26 (25–27), abdomen 16 (16–16), forewing 34 (33–36), hind wing 30 (28–32), antennae 22 (21–24).

Head. Occiput glossy, dark reddish brown, sometimes with yellow splotches. Postorbital sclerite dark reddish brown or dull brownish yellow. Vertex pattern slightly asymmetrical from side to side, lateral plates large, dark reddish brown or dull brownish yellow, dark regions bearing a sparse coat of long, very slender, pale yellow setae. Anterior extra-torular sclerites pale yellow or dark brownish red and concolorous with frons. Frons dark reddish brown, yellowish brown in some females, setae dark brown. Clypeus pale or dull yellow to dark reddish brown, setae dark brown. Paraocular band dark dusky or reddish brown. Anterior tentorial pit closed. Posterior genal triangle dull yellowish to dark reddish brown. *Mouthparts*. Labrum dark amber or reddish brown, setae dark brown. Mandibles dark reddish brown, bearing medium length thin dark brown setae, apices very dark brown. Maxillary stipes and palpomeres dull amber to dark reddish brown, stipes and palpomere 1 setae dark brown. Labium: submentum and mentum yellow to dark reddish brown, setae dark brown; labial palpi amber to reddish brown; ligula reddish brown. *Eyes.* Golden to dark reddish brown. *Antennae.* Scape dark reddish brown, setae dark brown. Pedicel dark reddish brown, distal margin often a pale red ring. Flagellum with 26–29 flagellomeres, evenly brown, flagellomere nodes sometimes thinly pale, occasionally darker than internodes, setitori undeveloped. Club with 11–14 flagellomeres, color yellowish with a thin diffuse dark longitudinal line anteriorly, slightly darkened posteriorly.

Thorax (A1 Fig. 99). *Cervix*. Dorsal cervical plates dark brown in males and one female, orange with a dark brown mesal macula in two females, setae brown. Cervical sclerite yellow to pale or dull yellow or orangish brown, anterior subapical setae dark brown. Ventral cervical plate ovoid, pale or dull yellow or brownish, setae brown. *Pronotum*. Color often evenly dark brown, but sometimes patterned, with somewhat numerous, long dark brown, very slender, setae. Prescutum completely brown or yellow along median sulcus and laterally. Scutum completely dark brown or diffusely yellowish sublaterally, posterolateral knob dark brown, bearing numerous long dark, very slender, setae. Scutellum either completely brown, or primarily yellow but with dorsal surfaces sublaterally transversely dark brown, bearing numerous long, very slender, dark brown setae. *Mesonotum*. Color pattern variably expressed. Prescutum lobes dark brown, with a round yellow spot on posterior surface and another on lateral surface of each lobe, entire surface bearing long, very slender, dark brown setae. Scutum dark brown with numerous yellow maculae, yellow patterning somewhat variably expressed, sometimes very weakly: yellow laterally near wing base, surrounding velvety spot and in a long stripe posterad of it, narrowly sagitally, and sublaterally along posterior margin, anterior and lateral surfaces bearing long, very slender, dark brown setae, dorsal surfaces bearing primarily white setae with a few dark setae intermingled. Scutellum dark brown, yellow laterally, along posterior margin, and as a broad sagital stripe widening slightly anteriorly and more so posteriorly, dorsal surfaces bearing sparse, long thin, very slender, dark brown setae, posterior margin bearing long thin white setae. Subscutellum yellow to brown. Postnotum brown, sometimes parasagitally yellow, glabrous. *Metanotum*. Paraprescutum yellow, or brown and concolorous with prescutum, glabrous. Prescutum dark brown, sometimes mostly yellow but mesally brown, surface with almost imperceptible sparse, very slender, pale setae. Scutum dark brown, sometimes with diffuse yellowish macula mesally, microtrichia cinnamon brown, posterior surfaces bearing long, very slender, white setae. Scutellum completely dark brown, or mostly yellow with sublateral dark brown maculae, sagitally glabrous, parasagittal surfaces bearing long, very slender, dark brown setae, posterolateral surfaces with long, very slender, white setae, posterior margin glabrous. *Pleuron*. Pleurites evenly brown to dark brown, mesobasisternite sometimes yellow dorsally, entire pleuron bearing a moderately thick coat of long, very slender, brown setae.

Legs. Coxal setae dark brown. Femora and tibiae reddish brown, or pale yellowish with reddish brown spots at bases of setae, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long stiff black; FV: short slender stiff black; FAL: short slender stiff black; FPL: long stiff black; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow; TPL: long thin stiff black; *mesothoracic leg setae*: FD: stiff medium short black; FV: stiff medium short black; FAL: very short thin black; FPL: long stiff black; TD: in distal half, sparse stiff medium length black; TV: long stiff black; TAL: medium short stiff black; TPL: medium short stiff black; *metathoracic leg setae*: FD: very short stiff slender black; FV: very short stiff slender black; FAL: long stiff black; FPL: long stiff black; TD: short stiff black; TV: medium long stiff black; TAL: medium long stiff black; TPL: medium long stiff black. *Tarsi*. Reddish brown.

Wings (A1 Figs. 97, 98, 100). C, Sc and sometimes R translucent reddish or brownish yellow, proximal third to half of Sc+R and distal 2-4 pterostigmal veinlets creamy yellow, most remaining veins, veinlets and crossveins brown to dark brown, others yellowish, a few veinlets and crossveins near wing base sometimes yellow. Rs with three clear forks. Ambient vein and axillary cord setae dark brownish gray. *Forewing*. Costal area slightly expanded in proximal third of wing, gradually narrowing such that C and Sc become approximately parallel past midpoint to pterostigma. Pterostigma comprising four to six often branched veinlets, proximal two to four cells suffused with brown to very dark reddish brown pigment, distal two to four cells more-or-less filled with opaque cream pigment, proximal cream-filled cells often sprinkled with dark pigment. Apical area containing four to six branched and unbranched veinlets, with 9 to 15 crossveins. Sc space without crossveins. Five to eight regular presectoral crossveins, rarely these connected by irregular crossveins. Cubital triangle with four to seven pre-fork crossveins, distal domain comprising two to four irregular cells. A single triangular or trapezoidal marginal cell present, sometimes connected to fork by a crossvein. Cup+1A anastomosis position more than two thirds distance from origin to Cu fork. 2A+3A diverging into one or more irregular forks in proximal half of anal area. Anal area with several oblique veinlets and crossveins. Anal angle ca. 45 degrees of wing axis, essentially straight. Posterior wing margin immediately distad of anal angle broadly and shallowly concave, becoming broadly and weakly convex in cubital area, narrowing slightly at Mp_1 and very slightly at Rs_1. *FW maculation*. Conspicious margining on crossveins of anal area, cubital triangle, in proximal portion of cubital area, and often on at least some of the other veinlets subtending proximal post- cubital fork half of Mp_2+Cua_1; a more distinct but broken longitudinal band of maculations formed from loose elongate aggregates of margining and cell darkening in proximal half of cubital area originating from point where Cua_2 strikes posterior wing margin, in postsectoral area near where Mp_1 begins to curve more sharply toward posterior wing margin, and in distal portion of radial area posterad of pterostigma and near posterior wing margin; a small macula in or slightly proximal of distal portion of apical area, sometimes weakly expressed; in males, radial area often with additional margining of many veinlets and crossveins, including those subtending R, and throughout other parts of wing. Male apical pigment patch (A1 Fig. 100) white and subtily distinguishable from cream in distal portion of pterostigma, commencing at pterostigma and filling apical area except for distal-most one fourth to one third, spilling into one to three rows of cells subtending Sc+R and often into compressed domain of subapical field, not reaching posterior wing margin. *Hind wing*. Costal area slightly expanded in proximal fourth of wing, then narrowing such that C and Sc become approximately parallel to pterostigma. Pterostigma comprising five to seven often branched veinlets, sometimes with very irregular crossveins, proximal two to four cells suffused with brown to very dark reddish brown pigment, distal two to four cells more-or-less filled with opaque often very pale cream pigment, proximal cream-filled cells often sprinkled with dark pigment. Apical area containing three to five branched and unbranched veinlets, with 5 to 17 crossveins. Sc space without crossveins. Two to four presectoral crossveins. Medial triangle with four to seven pre-fork crossveins; distal domain with three to four cells. Two or three irregular trapezoidal or triangular marginal cells present, these sometimes sometimes divided into an additional cell by a short fork. Posterior wing margin slightly concave along posterior medial area, narrowing again at Mp_1. *HW maculation.* Very faint margining of veinlets comprising marginal cells at apex of medial triangle; two distinct maculations forming a broken longitudinal band comprised of aggregates of margining and cell darkening in postsectoral area near where Mp_1 begins to curve more sharply toward posterior wing margin and in distal portion of radial area posterad of pterostigma and near posterior wing margin; as in forewing a small macula in or slightly proximal of distal portion of apical area, sometimes weakly expressed.

Abdomen. Outlines of T2+T3 and S3 diverging distad; outlines of T4–T6 and S4–S6 and sometimes segment 7 converging. Tergites and sternites velvety cinnamon to dark glossy brown; in a few specimens, distal margins of all sternites and tergites yellow and T1 to proximal half of T3 underneath dorsal setae patch mottled to entirely yellow. S2–S3 bearing long, very slender, brown setae; dorsolateral surfaces of T1, dorsum of T2 and proximal half of dorsum of T3 bearing a dense patch of medium short, wispy, brilliant white setae. Ectoprocts dark brown, setae black. *Sexually dimorphic characteristics*. *Males*. Pulvini apices protruding slightly, yellow to reddish brown. *Females.* T9 mottled brown and pale brown.

Male terminalia (A1 Figs. 101, 102). 9th sternite posterior margin not projecting forward, square. Gonarcus dorsum distinctly arched subapically in lateral view. Paramere stem darkened, narrowed basally, reaching base of gonarcus, blades projecting beyond pelta one-third length of gonarcus, apicoventral margins projecting ventrad of paramere stem, recurving strongly, widely splayed laterad in distal view. Pelta conspicuous, dark, broadly almond-shaped, mesally depressed, ventrally acuminate, mesal pores numerous. Pulvini narrow, approximately one and a half to two times longer than width at base, widely separated, bearing long, stiff, slender brown setae, mesally glabrous. Gonosaccal membrane between pulvini with some setae mesally and ventrad of parameres. Hypandrium internum cone-shaped.

Female terminalia (A1 Figs. 103, 104). Distivalvae small, oblong, fused mesally but slightly separated. Membrane between para-linguellar folds and T8 plates with setae dense, short, slender, dark brown. Linguella dorsal bulb medium large, slightly coned or acorn-shaped, with dark brown setae, ventral sagittal ridge of tissue well-developed, broadening dorsad until co-equal in width to interdens, laterally lined with several stiff black setae. Interdens medium large, sclerotized, slightly wider than long, quadrate or widely spoon-shaped. Ventrovalvae medium large in size, shallowly invaginated dorsally; setae along dorsal margin short, dark brown, curved, robust; setae situated ventrad of dorsal margin forming a transverse band, very short, black, peglike; setae ventrad of transverse band dense, very short, slender, stiff, dark brown.

Variation. One female (JRJ_00025) has verticils on the first 3-4 flagellomeres. One male (JRJ_01202) has the antennae pale yellowish and the spots at the bases of the leg setae evident, as well as well-defined yellow coloration on the distal margins of the abdominal segments and lateral surfaces of the ectoprocts, but otherwise resembles other males in every aspect. These differences in coloration appear to a lesser extent in other individuals (JRJ_00023, JRJ_00025, JRJ_00027) that have paler or slightly more contrasting coloration overall, including on the antennae, thorax and abdomen, but do not seem to coordinate with other morphological features, nor geographic distribution, and seem to simply represent intraspecific diversity.

Natural history and immature stages.—Adult flight period: April to May (Michel 2000; Michel & Cadet 2009. The larvae are unknown. Michel (2000) indicates that specimens have been captured at lights.

Primary type.—

Allocormodes micheli n. sp.

—Holotype by present designation, ♂, USNM (A1 Fig. 97). *Type locality*: Nigeria, Dada (town) [8.150000°, 4.000000°], 381 masl. *Label data*: “NIGERIA: Dada J. C. Geest, coll. /// Allocormodes maculipennis (Tasch.) ♂ det. Bo Tjeder 1981 /// HOLOTYPE Allocormodes micheli Jones ♂ design. J. R. Jones 2013 /// JRJ_00023”. Condition: excellent, antennae and wings spread, right mesothoracic tarsus missing.

Additional material examined (paratypes).—*Burkina Faso*: 3 males, 1 female [CIRAD: JRJ_00021, JRJ_00022, JRJ_00024, JRJ_00026]. *Mali*: 2 females [CIRAD: JRJ_00025 (A1 Fig. 98), JRJ_00027]. *Nigeria*: 1 male [BMNH: JRJ_01202].

Discussion.—This species is, based on average FW length and other measurements, the smallest in the genus. Its wing patterns are most similar to those of *A. nigris*, but it can be distinguished from the latter by the posterior fringes of white setae on the pteronotum.

Allocormodes nigris *n. sp.*

(A1 Figs. 105–110, 122)

Etymology and nomenclatural notes.—from *niger* (Latin), ‘black, dark, dusky’; adjectival. This species is named for the overall dark appearance attributed to both melanism, as expressed in the dark wings of the males, and the dark setae born on the pteropleuron and base of abdomen which both contrast with the paler dorsum.

Diagnosis.—Cervical sclerite apical knob brown; thorax and base of abdomen with thick brown pleural setae and grayish white dorsal setae, giving body the appearance of having a broad longitudinal dorsal stripe; males, in melanistic individuals, with most veins margined and cells fuscous in anterior two-thirds of wings; FW pterostigma mostly cream; distribution: Sub-Saharan tropical belt.

Proposed autapomorphies.—Cervical sclerite apex brown.

Distribution (A1 Fig. 122).—North and western Congo River drainage: Central African Republic, Congo.

Description.—

Size (mm). Male: body length 28 (25–31), abdomen 16 (15–18), forewing 37 (35–38), hind wing 31 (30–31), antennae 24 (22–25). Female: unknown.

Head. Occiput glossy, dark reddish brown, with a large yellow triangular plate-like splotch along postorbital sclerite margin ventrad of vertex plates. Postorbital sclerite dull yellowish brown. Vertex pattern slightly asymmetrical from side to side, lateral plates large, dull brownish yellow, dark regions bearing silvery microtrichiaand a sparse coat of long, very slender, dark brown setae. Anterior extra-torular sclerites pale yellow.

Frons reddish brown, setae dark brown. Clypeus dull reddish brown, setae brown. Paraocular band dark brown adjacent to antennae, orangish brown mesally, dull yellow near mandible bases. Anterior tentorial pit open or closed. Posterior genal triangle dull yellowish. *Mouthparts*. Labrum dark reddish brown, setae dark brown. Mandibles dark reddish brown, bearing medium length thin dark brown setae, apices very dark brown. Maxillary stipes dull dark reddish brown, palpomeres dull brownish amber, stipes and palpomere 1 setae dark brown. Labium: submentum and mentum dark reddish brown, setae dark brown; labial palpi dull amber brown; ligula dull reddish brown. *Eyes*. Golden brown. *Antennae*. Scape dark reddish brown, setae dark brown. Pedicel dark reddish brown, distal margin a brownish orange ring. Flagellum with 27–28 flagellomeres, evenly pale to dark brown, flagellomere apices darker, distal margins thinly pale, occasionally darker than internodes, short black setae more prominent in distal third of flagellum, setitori at most very slightly developed. Club with 11–12 flagellomeres, dark brown, mesoventrally and sometimes dorsally yellow, setae bases within yellow areas dark brown.

Thorax (A1 Fig. 107). *Cervix*. Dorsal cervical plates pale orange, setae dark brown. Cervical sclerite dull dark reddish brown, anterior subapical setae dark brown. Ventral cervical plate, oblong, yellow, setae brown. *Pronotum*. Setae somewhat numerous, long, dark brown, wispy. Prescutum yellow dorsally and laterally, dark brown sublaterally. Scutum mostly dark brown, yellowish sublaterally, integument at setal bases in yellow area dark brown, posterolateral knob dark brown. Scutellum dorsal surfaces dark brown, thinly yellow sagitally, bearing numerous long, very slender, dark brown setae, posterior surface invaginated, yellow. *Mesonotum*. Prescutum lobes dusky dark brown, with a diffuse round orange spot on anterolateral surface and another on posterior surface of each lobe, entire surface bearing long, very slender, dark brown setae, integument at bases of setae on edges of orange portions marked with dark brown. Scutum dusky dark brown with several weakly expressed yellowish maculae: orange laterally near wing base, on anterior margin of velvety spot, a short thin stripe posterad of it, and a thin transverse sagittal line along anterior margin, and sometimes mesally on each lobe adjoining margin of scutellum, anterior and lateral surfaces bearing, very slender, brown setae, dorsal and posterior surfaces bearing grayish white setae. Scutellum dark brown, orange posterolaterally, as a broad sagital stripe on posterior bulge, and along posterior margin of posteror bulge, anterodorsal surface glabrous, posterior and lateral surface of anterior and posterior bulge bearing sparse, long thin, very slender, mixed grayish white and dark brown setae. Subscutellum orangish yellow, diffusely brown sagitally. Postnotum brown, glabrous. *Metanotum*. Paraprescutum yellow dorsally, brown laterally, glabrous. Prescutum cinnamon brown with lateral margins diffusing into orange and bearing long thin, very slender, mixed grayish white and dark brown setae, integument at their bases marked with dark brown. Scutum dark brown, orange on mesal surface of lobes, microtrichia cinnamon brown, posterior surfaces bearing long, very slender, brown setae. Scutellum dark brown, lateral margins orange, sagittally with diffuse thin orange line with sublateral dark brown maculae, dorsally glabrous, lateral and posterior surfaces bearing long, very slender, grayish white setae intermixed with a few brown setae. *Pleuron*. Pleurites evenly brown, entire pleuron bearing a thick coat of long, very slender, brown setae.

Legs.—Coxal setae dark brown. Femora reddish brown; tibia proximal third of dorsal surface dull yellowish brown, terminally marked by a transverse dark reddish brown line, remaining surfaces yellow with reddish brown spots at bases of setae, spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long, stiff black; FV: short slender stiff black; FAL: short slender stiff black; FPL: long, stiff black; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow; TPL: long thin stiff black; *mesothoracic leg setae*: FD: obscured but apparently long stiff black; FV: obscured but apparently long stiff black; FAL: obscured; FPL: long stiff black; TD: in distal half sparse stiff medium length black; TV: long stiff black; TAL: medium short stiff black; TPL: medium short stiff black; *metathoracic leg setae*: FD: mixed long slender black and long stiff black; FV: mesolongitudinally glabrous; FAL: long stiff black; FPL: long stiff black; TD: short stiff black; TV: laterally divergent long stiff black; TAL: short stiff black; TPL: short stiff black. *Tarsi.* Reddish brown.

Wings (A1 Figs. 105, 106, 108). All wing apices very slightly asymmetrical and subacute. Longitudinal veins and most veinlets and crossveins brown to dark brown, some tinged with diffuse yellow; in FW, C from wing base to pterostigma reddish brown or yellow, otherwise dark brown, yellow color also in pterostigma veinlets, along proximal two thirds of Sc+R and apical area veinlets, and on veinlets and crossveins near apex of cubital triangle. Rs with three clear forks. Ambient vein and axillary cord setae dark brown. *Forewing*. Costal area slightly expanded in proximal third of wing, then very gradually narrowing until just proximad of pterostigma, then expanding slightly around pterostigma. Pterostigma pigment long and broadly spindle-shaped, traversing six to eight veinlets, distal veinlets often branched, proximoventral margin of pigment with dark reddish brown granules, remaining pigment cream yellow. Apical area containing five to seven branched and unbranched veinlets, with 17 to 25 crossveins. Sc space without crossveins. Five to seven presectoral crossveins. Cubital triangle with five to seven pre-fork crossveins, distal domain comprising three to four irregular cells. A single triangular or trapezoidal marginal cell present, sometimes connected to fork by a crossvein. Cup+1A anastomosis position half to two thirds distance from origin to Cu fork. 2A+3A very robust, diverging into one or more irregular forks in proximal half of anal area. Anal area with several oblique veinlets and crossveins. Anal angle ca. 45 degrees of wing axis, essentially straight. Posterior wing margin posterad of cubital triangle slightly concave, posterior wing margin of cubital area slightly expanded and curving, narrowing again at Mp_1 and again very slightly at Rs_1. *FW maculation*. In melanistic specimens, nearly all veins, veinlets and crossveins margined and all cells fuscous in anterior two-thirds of wing, except in proximal two-thirds of apical area and compressed domain of subapical field, although marginal cells of subapical field fuscous, and thickest margining on veinlets subtending R, anal area, distal half of cubital triangle, post-fork portion of cubital area, mesal and distal portions of cubital area along posterior edge of pigmentation, distal portions of post-sectoral and radial areas along posterior edge of pigmentation; in non-melanistic specimen, irregular maculation arranged linearly, veinlets and crossveins most conspicuously margined in anal area, in mesal and distal portions of cubital area, in distal portions of post-sectoral and radial areas, and in apical portion of apical area. Male apical pigment patch (A1 Fig. 108), occupying proximal two-thirds of apical area, first cell row subtending Sc+R, margins of second row, and compressed domain of subapical field, not reaching posterior wing margin. *Hind wing*. Costal area slightly expanded in proximal fourth of wing, then narrowing until C and Sc parallel at midpoint to slightly proximad of pterostigma, then expanding again. Pterostigma pigment long and broadly spindle-shaped, traversing seven to eight branched and unbranched veinlets, proximal three to five cells suffused with dark brown pigment, this opaque and very dark in melanistics, distal cells with opaque cream yellow pigment, often sprinkled with dark granules where they adjoin darker cells and mesally within cells, ventral margin along Sc lacking dark pigment in all cells. Apical area containing four to six branched and unbranched veinlets, with 14 to 22 crossveins. Sc space without crossveins. Four to six presectoral crossveins. Medial triangle with four to six pre-fork crossveins; distal domain with four cells. One or three irregular trapezoidal or triangular marginal cells present. Apical cell of anal area proximad of triangle marginal cells large, often containing a single spurious vein. Posterior wing margin slightly concave, narrowing slightly at Mp_1 and Rs_2. *HW maculation.* In melanistic specimens, nearly all veins, veinlets and crossveins margined and all cells fuscous in anterior two-thirds of wing, except in proximal two-thirds of apical area and compressed domain of subapical field, although marginal cells of subapical field fuscous; thickest margining on veinlets subtending R, distal portions of post-sectoral and radial areas along posterior edge of pigmentation, and in apical area at distal edge of pigmentation; in non-melanistic specimen, veinletes and crossveins margined in distal portions of post-sectoral, radial, and apical areas.

Abdomen. Outlines of T2+T3 and S3 diverging distad; outlines of T4–T6 and S4–S6 converging. Tergites dark cinnamon brown, sternites dark brown; T2 diffusely orange or yellowish underneath setae; distal margin of S3 sublaterally very diffusely paler brown; distal margins of tergites and some sternites slightly paler brown. Dorsal and lateral surfaces of T1 to proximal two-thirds of T3 bearing long, very slender, setae, lateral setae brown and dorsal setae mixed grayish white and brown; pleural membranes of T2–T3 bearing very thick coat of long, very slender, brown setae; S2–S3 bearing long, very slender, brown setae. Ectoprocts dark brown, setae brown. *Sexually dimorphic characteristics*. *Males*. Pulvini apices not protruding in undissected specimen (JRJ_01212), orangish. *Females.* Unknown.

Male terminalia (A1 Figs. 109, 110). 9th sternite posterior margin not projecting forward, square. Gonarcus dorsum arched in lateral view. Paramere stem darkened, not narrowed basally, reaching base of gonarcus, blades projecting beyond pelta one-third length of gonarcus, apicoventral margins projecting ventrad of paramere stem, recurving, splayed laterad in distal view. Pelta conspicuous, dark, narrowly almond-shaped, mesally depressed, ventrally blunt, mesal pores numerous. Pulvini narrow, approximately one and a half times longer than width at base, widely separated, bearing medium-long, stiff, slender brown setae, mesally glabrous. Gonosaccal membrane between pulvini with some setae mesally. Hypandrium internum extensively but thinly sclerotized bilaterally.

Female terminalia. Unknown.

Variation. Left FW of JRJ_01198 has two Rs veins. JRJ_00028 is not melanistic and is slightly smaller, but otherwise matches the melanistic specimens well. Its wings are very slightly more slender than the two melanistic individuals, and its hind femora are pale with reddish brown spots. Its apical pigment patches also display less white pigment, although this may be due to wear and tear in life, and the distribution of the patch in the wing can be seen clearly.

Natural history and immature stages.—The biology of this new species is unknown.

Primary type.—

Allocormodes nigris n. sp.

—Holotype by present designation, ♂, MNHN (A1 Fig. 105). *Type locality*: Central African Republic, La Mbaïki (city) [3.865685°, 17.994289°], 502 masl. *Label data*: "LA MABOKE REP. CENTRAFRIC. P.L. 5-II-1970 Michel BOULARD /// HOLOTYPE Allocormodes nigris Jones ♂ design. J. R. Jones 2013 /// JRJ_01212". *Condition*: excellent, antennae forward, wings spread, mesothoracic legs missing, right HW membrane with some small holes near pterostigma, left FW tip slightly torn.

Tjeder was the first to recognize the distinctions of this species, as indicated by the holotype label with his name on the BMNH specimen. This study confirms the specimen's uniqueness and, thus, it is here described; however, the MNHN specimen is in much better condition and has been selected as the holotype.

Additional material examined (paratypes).—*Congo*: 1 male [BMNH: JRJ_01198]. *Guinea*: 1 male [MFNB: JRJ_00028 (A1 Fig. 106)].

Discussion.—The female of this infrequently collected species is unknown. The melanistic male is very conspicuous by virtue of its darkened wings, which in this regard resemble those of *A. kolbei*, and is the only other *Allocormodes* species in which strong melanism has been observed. If *A. nigris* displays sexual dimorphism similar to *A. kolbei*, the female, when discovered, will not have darkened wings. However, it is interesting to note that the fuscous appearance of the wings of the two melanistic specimens examined for this study is nearly identical, despite the 1100 kilometer separation of their collecting localities.

Allocormodes nigristigma *n. sp.*

(A1 Figs. 111–119)

Etymology and nomenclatural notes.—from *niger* (Latin), 'black, dark, dusky'; *stigma* (Latin) 'spot, mark'; noun in apposition. This species is named for the dark pterostigmata of the hind wing.

Diagnosis.—Most pterothoracic setae brown, but mesal surface of metascutal lobe marked by a yellowish maculae bearing pale yellow, very slender, setae; FW anal angle of males convex from wing base to posterior wing margin. HW pterostigma elongate and entirely dark; thorax lacking patch of white setae behind velvety spots; distribution: sub-Saharan tropical belt.

Proposed autapomorphies.—HW pterostigma pigment completely very dark brown.

Distribution (A1 Fig. 119).—Sub-Saharan tropical belt: Cameroon, Democratic Republic of the Congo, Gabon, Guinea, Liberia, Nigeria, Sierra Leone, Uganda. *Notes*: With *A. intractabilis* and *A. maculipennis*, *A. nigristigma* has one of the broadest distributions of all *Allocormodes* species.

Description.—

Size (mm). Male: body length 29 (26–32), abdomen 15 (13–17), forewing 25 (33–37), hind wing 29 (28–30), antennae 23 (21–25). Female: body length 25 (22–28), abdomen 14 (12–16), forewing 38 (37–40), hind wing 34 (32–35), antennae 23 (22–25).

Head. Occiput pale to dark reddish brown, diffusely yellow near postorbital sclerite. Postorbital sclerite dull, color variable, dark reddish brown to orangish to brownish yellow. Vertex pattern slightly asymmetrical from side to side, lateral plates variable in shape, yellow to dull orangish brown, dark regions bearing silvery microtrichiaand a sparse coat of long, very slender, brown setae. Anterior extra-torular sclerites yellow. Frons very pale reddish brown, occasionally darker, setae dark brown. Clypeus yellowish to dark reddish brown, setae dark brown. Paraocular band dusky yellowish to dark reddish brown. Anterior tentorial pit closed. Posterior genal triangle dull yellowish to dark reddish brown. *Mouthparts*. Labrum dark reddish brown, setae medium long, dark brown. Mandibles dull yellow to reddish brown, setae black. Maxillary stipes and palpomeres dull amber to dark reddish brown, stipes and palpomere 1 setae dark brown. Labium: submentum and mentum amber to dark reddish brown, setae dark brown; labial palpi amber to reddish brown; ligula granularly reddish brown. *Eyes*. Golden to dark reddish brown. *Antennae*. Scape reddish brown to dark brown, setae dark brown. Pedicel dark reddish brown, distal margin often a pale red ring. Flagellum with 26–27 flagellomeres, pale yellowish brown basally, darkening in distal half, flagellomere nodes sometimes darker than internodes, setitori undeveloped. Club with 11–12 flagellomeres; color yellowish with a thin diffuse dark longitudinal line anteriorly and posteriorly.

Thorax (A1 Fig. 113). *Cervix*. Dorsal cervical plates yellow to dull orange with a dark brown mesal macula, setae brown. Cervical sclerite apically and ventrally yellow to dull orange, dorsal subapical surface dark brown, anterior subapical surface setae dark brown. Ventral cervical plate ovoid, dull yellowish brown to dark brownish. *Pronotum*. Prescutum brown sublaterally, yellow sagitally and laterally. Scutum dark brown, posterolateral knob dark brown. Scutellum dorsal surface dark brown, anterolateral surface with small yellow macula, yellow sagitally and posteriorly, setae numerous, long, wispy, dark brown. *Mesonotum*. Prescutum dark brown, lobes with a round yellow or orange macula on posterior surface and another on lateral surface, entire surface bearing medium long, very slender, dark brown setae. Scutum dark brown, yellow or orange macula laterally near wing base, two maculae posterad of velvety spot near posterior wing margin, all surfaces bearing long, very slender, dark brown setae.

Scutellum dark brown, a yellow macula on posterolateral surface of anterior bulge, and as a sagittal and lateral macula on posterior bulge, dorsal surfaces bearing sparse, long thin, very slender, dark brown setae, posterior margin bearing long thin white setae. Subscutellum orangish, dark brown sagitally. Postnotum dark brown, glabrous. *Metanotum*. Paraprescutum brown, glabrous. Prescutum brown, with sparse, very slender, brown setae. Scutum dark brown, mesal surface of bulge with yellowish macula mesally, this bearing mixed pale yellowish and dark brown, very slender, setae, microtrichia cinnamon brown, other surfaces with long, very slender, brown setae. Scutellum dark brown, laterally yellow or orange, sagitally glabrous, posterolateral surfaces bearing long, very slender, dark brown setae. *Pleuron*. Pleurites evenly brown, bearing a moderately thick coat of long, very slender, brown setae.

Legs. Coxal setae dark brown. Femora (prothoracic and sometimes mesothoracic) reddish brown, or pale yellowish with reddish brown spots at bases of setae; tibia pale yellowish with reddish brown spots at bases of setae, tibial spurs reddish brown; setae as follows: *prothoracic leg setae*: FD: long stiff black; FV: short slender stiff black; FAL: short slender stiff black; FPL: long stiff black; TD: medium length stiff black; TV: medium length stiff black; TAL: preening patch setae golden yellow; TPL: long thin stiff black; *mesothoracic leg setae*: FD: stiff medium short black; FV: stiff medium short black; FAL: very short thin black; FPL: long stiff black; TD: in distal half, sparse stiff medium length black; TV: long stiff black; TAL: medium short stiff black; TPL: medium short stiff black; *metathoracic leg setae*: FD: very short stiff slender black; FV: very short stiff slender black; FAL: with long stiff black; FPL: with long stiff black; TD:

short stiff black; TV: medium long stiff black; TAL: medium long stiff black; TPL: medium long stiff black. *Tarsi.* Yellowish to reddish brown.

Wings (A1 Figs. 111, 112, 114). Veins, veinlets and crossveins mostly yellowish or reddish brown to dark brown, some variably yellow, FW Sc+R yellow. Rs with at least three unambiguous forks. Ambient vein and axillary cord setae brown. *Forewing*. Costal area expanded in proximal third of wing, gradually narrowing such that C and Sc become approximately parallel approximately three-fifths distance from wing base to pterostigma. Pterostigma somewhat elongate, comprising six to seven sometimes branched veinlets, proximal three to five cells suffused with brown to very dark reddish brown pigment, last cells mixing with cream pigment, distal one to three cells more-or-less filled with opaque cream pigment. Apical area containing four to six branched and unbranched veinlets and 16 to 22 crossveins. Sc space without crossveins. R subtending crossveins not widely spaced, spacing slightly wider in some females. Five to eight regular presectoral crossveins, rarely these connected by irregular crossveins. Cubital triangle with five to seven prefork crossveins; distal domain comprising three to four often irregular cells. Usually a single triangular marginal cell, sometimes connected by a crossvein. Cup+1A anastomosis more than four fifths distance from origin to Cu fork, Cup and 1A connected by one to four short and usually dark veinlets. 2A+3A very robust, diverging into one or more irregular forks in proximal half of anal area. Anal area with several oblique veinlets and crossveins. Anal angle ca. 45 degrees of wing axis, essentially straight, not produced, very smoothly sloping to posterior wing margin in males. Posterior wing margin posterad of cubital triangle very slightly concave, more so in females, posterior wing margin of cubital area very slightly expanded and curving, narrowing again at Mp_1 and again very slightly at Rs_1. *FW maculation*. Conspicious margining on at least a portion of the length of most veinlets and crossveins throughout wing, except for apical area and compressed domain of radial area; margining generally slightly more expressed in males; a small macula in or slightly proximal of distal portion of apical area, sometimes weakly expressed; cells becoming fuscous in mesobasal portion of cubital area and in distal portions of radial area near wing margin. Male apical pigment patch (A1 Fig. 114) commencing at pterostigma and filling apical area, extending posterad of pterostigma in subapical field of radial area, including over compressed domain, not reaching posterior wing margin, pigment sometimes worn away. *Hind wing*. Costal area conspicuously expanded at base of wing, then narrowing such that C and Sc become approximately parallel just beyond midpoint, until beginning to expand again immediately proximad of pterostigma. Pterostigma elongate, comprising seven to nine sometimes branched veinlets, pigment almost entirely dark, mixed with slightly paler to cream in distal one or two cells. Apical area containing four to six branched and unbranched veinlets and 9 to 25 crossveins. Sc space without crossveins. Three to seven presectoral crossveins. Medial triangle with four to six pre-fork crossveins; distal domain comprising three to six cells. Two or three irregular trapezoidal or triangular marginal cells present. In males, posterior wing margin conspicuously convex to near midpoint of posterior medial area, which is very slightly concave. *HW maculation*. Scattered faint margining of some veinlets and crossveins throughout wing, but most conspicuous margining throughout radial area and in distal portions of radial and postsectoral areas, the latter wherein the cells are also fuscous; a small macula in or slightly proximal of distal portion of apical area, sometimes weakly expressed; in males, radial area proximad of pterostigma with many veinlets and crossveins margined.

Abdomen. Outlines of T2+T3 and S3 diverging distad; outlines of T4–T6 and S4–S6 and sometimes segments 7 and 8 converging. Tergites and sternites velvety cinnamon to dark glossy brown, distal margins of sternites and tergites pale brown to yellow, T1 to proximal half of T3 very subtily paler mottled brown. S2 to proximal half of S3 bearing long, very slender, brown setae; dorsolateral surfaces of T1 bearing long, very slender, brown setae, apparently lighter in color in females; dorsum of distal half of T2 and proximal half T3 bearing a patch of medium short, wispy, pale yellow setae. Ectoprocts dark brown, setae black. *Sexually dimorphic characteristics*. *Males*. Pulvini apices protruding, yellow to reddish brown. *Females.* T9 variable, brown to dark brown, mesodistal margin often with a diffuse pale brown macula, a thin dorsal pale brown macula sometimes also present.

Male terminalia (A1 Figs. 115–116). 9th sternite posterior margin very slightly projecting forward, obtuse. Gonarcus dorsum arched apically in lateral view. Paramere stem darkened, not narrowed basally, not reaching base of gonarcus, blades projecting beyond pelta one-sixth length of gonarcus, apicoventral margins projecting ventrad of paramere stem, not recurving, splayed laterad in distal view. Pelta conspicuous, dark, almond-shaped, ventrally blunt, mesally depressed, mesal pores minute. Pulvini narrow, approximately three to four times longer than width at base, widely separated, bearing long, stiff, slender dark brown setae, mesally glabrous. Gonosaccal membrane between pulvini with several setae mesally and also ventrad of parameres. Hypandrium internum thinly sclerotized along corners of basket-like shape.

Female terminalia (A1 Figs. 117–118). Distivalvae small, ovoid, fused mesally but slightly separated. Membrane between para-linguellar folds and T8 plates with setae dense, short, slender, dark brown. Linguella dorsal bulb medium large, slightly coned or acorn-shaped, with dark brown setae, ventral sagittal ridge of tissue developed. Interdens small, sclerotized, longer than wide, spoon-shaped. Ventrovalvae medium small, shallowly invaginated dorsally; setae along dorsal margin short, brown, curved; setae situated ventrad of dorsal margin forming a transverse band, very short, brown, curved; setae ventrad of transverse band dense, very short, slender, stiff, dark brown.

Variation. Some specimens have slightly paler legs, and one of these appears teneral (JRJ_00045). HW pterostigma pigment is paler and more weakly expressed in JRJ_01215 and JRJ_00045.

Natural history and immature stages.—One specimen (JRJ_01208) bears a label indicating it was collected at a light. The larvae are unknown.

Primary types.—

Allocormodes nigristigma n. sp.

—Holotype by present designation, ♂, UMSP (A1 Fig. 111). *Type locality*: Cameroon, 3 km ESE Bindom (town) [2.672000°, 13.257167°], 661 masl. *Label data*: “AFRICA: Cameroon Zoulabot, 2 km E Minton 02°40.32’ N, 013°15.43’ E July 20-25, 2001 P.J.

Clausen /// HOLOTYPE Allocormodes nigristigma Jones ♂ design. J. R. Jones 2013 /// JRJ_00029". *Condition*: excellent, antennae and wings spread, left antennae apex slightly nicked, left metathoracic leg missing.

This specimen is in the best condition of all those examined. Esben-Petersen was apparently the first to recognize the distinctness of this species as indicated by his holotype label attached to one of the examined specimens (JRJ_01201), but no record of a description of it by him has been found.

Additional material examined (paratypes).—*Democratic Republic of the Congo*: 3 males, 2 females [RMCA: JRJ_01169, JRJ_01170, JRJ_01175, JRJ_01167, JRJ_01192]. *Gabon*: 1 male, 1 female [MNHN: JRJ_01216, JRJ_01215]. *Guinea*: 1 female [CIRAD: JRJ_00047 (A1 Fig. 112)]. *Liberia*: 1 female [USNM: JRJ_00045]. *Ivory Coast*: 1 female [RMCA: JRJ_01174]. *Nigeria*: 1 male, 1 female [BMNH: Nigeria, JRJ_01208, JRJ_00041]. *Sierra Leone*: 1 male [EMUS: JRJ_00040]. *Uganda*: 2 males, 1 female [BMNH: 2 males, JRJ_01196, JRJ_01201; MFNB: 1 female, JRJ_00046]. *Locality uncertain*: 2 males, 1 female [RMCA: JRJ_01194, JRJ_01195, JRJ_01161].

Discussion.—Undissected, *A. nigristigma* is one of the most difficult species in the genus to distinguish, particularly from *A. maculipennis*, *A. micheli* and *A. inconspicuus*, and the material examined bears previous workers' determination labels as *A. intractabilis*, *A. kolbei*, and *A. maculipennis*. At the present time only a single autapomorphic feature is known for *A. nigristigma*, the completely dark hind wing pterostigmata, but in some paler specimens this feature may be difficult to diagnose. This species can also be recognized by its lacking the autapomorphies observed in the similar species *A. maculipennis* (triplet of margined veins in FW cubital area) and *A. micheli* (patches of white setae on pterothorax and basal abdominal tergites). Examination of genitalia, particularly of the female, may be required for positive identification.

Final thoughts and future research

This study, in addition to discovering several new species, re-describing the known taxonomic diversity of the genus, providing a thorough identification key, and resolving several nomenclatural issues, addressed larger questions of owlfly anatomy, feeding, and phylogeny, and in so doing contributes to a larger understanding of the morphology, biology, evolution and distribution of all Ascalaphidae.

Nevertheless, as with many genera of Ascalaphidae, *Allocormodes* is vastly undercollected, and the taxonomic results presented in this work are based on relatively few specimens. It is hoped that the findings reported here will stimulate future investigations into this charismastic group by facilitating more targeted collecting and correct identification of species.

Additional studies of this genus are needed in the following areas of research: (1) descriptions of immature stages of all species (eggs, larval instars, pupa, and cocoon); (2) increasing the number of specimen records and fleshing out the geographic distributions for each of the species; (3) acquisition of high-quality specimens for DNA analysis; (4) additional phylogenetic analyses incorporating molecular data; (5) biogeographic description and hypothesis testing; and (6) discovery and descriptions of the males of *A. albus* and *A. maynei*, and the female of *A. nigris*.

CHAPTER III

TAXONOMIC REVISION OF THE BROWN-BLOTCHED BLADEWING GENUS *TMESIBASIS* MCLACHLAN, 1871 (ASCALAPHIDAE: HAPLOGLENIINAE)

Synopsis

Tmesibasis is a genus of rather large and charismatic, but poorly understood, entire-eyed owlflies (Haplogleniinae) that is distributed across sub-Saharan Africa and the southwestern Arabian Peninsula. Before this revision, ten species were recognized, but the validity of several older species was dubious, genitalia had only been figured for two recently described species, no identification key had been published, and accurate identification of most species was very difficult. In this revision, eight of the previously-described species are recognized as valid, two species names, *Tmesibasis andruzzii* Navás and *Tmesibasis regia* Navás, are placed in synonymy with *Tmesibasis rothschildi* van der Weele, and two new species, *Tmesibasis majesta* and *Tmesibasis simplex*, are recognized. These ten species are described and figured, and keys to their identification and maps of their distributions are provided. An hypothesis of intrageneric relationships based on a cladistic analysis of 39 morphological characters is presented.

Introduction

Tmesibasis is an exceptionally charismatic but poorly understood genus of entire-eyed owlflies (Haplogleniinae) that is distributed across sub-Saharan Africa from Senegal to Somalia, south to South Africa, and north along the coastal areas of the southwestern Arabian Peninsula. Its species are moderately large, have very narrow wing bases and very long antennae, and display on their wings a conspicuous pattern of cinnamon-colored triangular blotches that circumscribe the margins.

From before the time of the initial description of the genus authors have been impressed with the dramatic appearance of its species. Hagen (1862) called his species *lacerata* "one of the finest and strangest known to [him]"; McLachlan (1871) stated that *Tmesibasis* was "without a parallel among the Holophthalmi"; van der Weele (1907) called the genus "le plus élégant des Ascalaphides"; and Navás (1912) referred to a species he described as "la plus belle parmi les Ascalaphides holophthalmes que j'aie vus". With dramatic patterns on their wings, thorax and abdomen, several species have been named after royalty—van der Weele (1909) designated one species *imperatrix* ("empress"), Navás (1912) named another *alberti*, after the king of Belgium, and still another (1915) *regia* ("queen").

Before this revision, ten species were recognized, but no identification key had ever been published and genitalia had only been figured for two recently described species. As several species are extremely similar, however, their validity has been dubious and their proper identification very difficult. In this study, eight of the previously-described species are recognized as valid; two species names are placed in synonymy, and two new species are presented. These ten species are described and figured, and keys to their identification and maps of their distributions are provided. A cladistic analysis was performed to investigate intrageneric species relationships.

Taxonomic history

The history of the genus begins with Hagen, who described (1853) and later figured (1862) *Ascalaphus laceratus* from Mozambique. McLachlan (1871), in his seminal revision of the Ascalaphidae, erected the new genus *Tmesibasis* to contain *laceratus*, based solely on Hagen's description and figure. Van der Weele (1907) described *rothschildi* from British and German East Africa. Shortly after, in his monumental monograph on owlflies, van der Weele (1909) presented the only published revision of *Tmesibasis*, in which he redescribed *lacerata* and *rothschildi* and added two new species, *imperatrix* and *waelbroecki*. In the years that followed, Navás described single new species in each of four publications (1912, 1915, 1929, 1933). Finally, Tjeder (1980) and Hölzel (1983) each also described single new species. The papers of the latter were the first to include descriptions and drawings of the male and female genitalia.

In the years prior to his untimely death in 1992, Tjeder had begun to revise the genus as part of his monograph of the Ascalaphidae of the Afrotropical region. Unfortunately, his work was never completed. Nevertheless, his assistant Hansson was able to move what had been finished through to publication (Tjeder and Hansson 1992); this included his nearly comprehensive and high-quality treatment of the African Haplogleniinae (Tjeder 1992), which covered all genera known at the time except for *Tmesibasis* and *Allocormodes*. Tjeder's revisionary efforts on *Tmesibasis* are evidenced by brick red type labels that he applied to the pins of some specimens he examined, which are present in several U.S. and European collections. From the unpublished names discovered on those labels, he appears to have planned to describe at least three new species. Although only one of those manuscript taxa was ultimately supported in this study, one can surmise that he would have made other changes, and there is no doubt that his contribution would have been significant and positive.

This study contains the first description of new *Tmesibasis* species since Hölzel (1983), and is only the second monographic revision of the genus ever undertaken.

Materials and methods

Material

The 90 specimens examined for this revision are contained in the research collections listed below. Most were pinned, but a few consisted of full-body macerations. This list also includes collections from which specimens were not borrowed but which are referenced in this work. These are marked with an asterisk (*).

AMGS	Albany Museum, Grahamstown, South Africa
BMNH	The Museum of Natural History (British Museum of Natural History), London, UK
CAS	California Academy of Sciences, San Francisco, California, USA
CIRAD	Centre de Coopération Internationale en Recherche Agronomique pour Le Développement, Montpellier, France
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA
HNHM	Hungarian Natural History Museum, Budapest, Hungary
IRSNB*	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MFNB	Museum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany
MHNG	Muséum d'histoire naturelle, Geneva, Switzerland

MNHN	Muséum national d'Histoire naturelle, Paris, France
MSNG*	Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy
NHMB*	Naturhistorisches Museum, Basel, Switzerland
NMW*	Naturhistorisches Museum Wien, Vienna, Austria
RMCA	Royal Museum for Central Africa, Tervuren, Belgium
TAMUIC	Texas A&M University Insect collection, College Station, Texas, USA
UCDC	R. M. Bohart Museum of Entomology, University of California, Davis, USA
UMMZ	Museum of Zoology – Insect Division, University of Michigan, Ann Arbor, Michigan, USA
USNM	Smithsonian National Museum of Natural History, Washington, D.C., USA

Specimen examination

Both pinned and dissected specimens were observed under a Leica MZ6 dissecting microscope enabling magnifications from 6.3 to 40 times.

Specimen preparation and dissections

Specimens were prepared following the protocols detailed in chapter 1.

Photography and illustrations

See chapter 1 for a detailed explanation of the methods used to capture photographs and create illustrations.

Terminology

Anatomical terminology has extracted from a number of sources, including Adams (1958), Aspöck et al. (1980), Penny (1982), New (1984), Tjeder (1992) and the Torre-Bueno Glossary of Entomology (Nichols 1989). In the course of this study it was also convenient to create some new descriptors specifically for *Tmesibasis* owlflies. These terms are listed and explained under 'Adult morphology', below.

Abbreviations and annotations

Acronyms and abbreviations are used throughout this text; a full treatment of terms represented by each acronym or abbreviation is provided in chapter 1. New acronyms not presented in chapter 1 appear in some figure captions and are defined therein.

Databasing

All specimens examined for this work have been assigned, and have had attached to their pin or placed in their cryogenic tube, a JRJ database number. See chapter 1 for a complete explanation of the database, its purpose, and the protocols followed for its development.

Adult morphology

The major anatomical structures and features of *Tmesibasis* owlflies are summarized in telegraphic style in the formal genus description under ‘Taxonomic treatment’, below. This morphology section focuses on presenting and defining new terms developed for this study (marked with an asterisk*), on discussing anatomical features of *Tmesibasis* that are unique among owlflies, and on expanding upon aspects of anatomy that do not fit cleanly within the formal descriptions, or that might not easily be gleaned from it.

Size/dimensions (A2 Excel File 2)

Tmesibasis are medium to large-sized owlflies (♂♂: FW lengths 24–33 mm; ♀♀: FW lengths 29–38 mm), with males slightly to considerably smaller than females in the various dimensions of the body and wings. The antennae of males, however, are proportionally longer—usually 1.2 to 1.25 times as long as those of females. The lengths of the abdomens of the sexes relative to their wing lengths are proportionally more-or-less coequal. However, there is much telescoping/shrinkage in dry specimens and live length is difficult to estimate; in this study dry length was measured. Female abdominal somites 4 through 7 are often considerably more expanded than in males. Wing shape is also sexually dimorphic, with the wings of males usually less falcate, and either broader or narrower, than those of females.

Head

Eyes (A2 Figs. 2–3). Surprisingly and curiously—in light of their traditional position within a Haplogleniinae presumed to be monophyletic on the basis of an entire eye—some species of *Tmesibasis* exhibit a slight transverse depression that weakly divides the surface of the eye posteriorly into an upper and lower portion. No accompanying transverse sulcus is present. The ocular foramen is circular; however, the ocular diaphragm is slightly flexed posteriorly, near the depression.

Antennae (A2 Figs. 4–6). The scape is typically subspherical, and the pedicel base is hemispherical. The flagellum expresses on its various faces near its base features that are useful in descriptions, but determining which surface is anterior or posterior, or dorsal or ventral, can be difficult to interpret. In examined dried specimens, the antennae are artificially oriented in all directions as a result of arrangement during curation (or from having been broken off and reglued to the specimen), such that the pedicel is oriented relative to the scape in slightly different positions, and the club is oriented in all directions relative to the scape and pedicel. Live specimens appear to hold their antennae in a distinct resting position, that is forward, somewhat to the side, and slightly raised relative to the body axis (Figs. 29, 30). With this live position in mind as a "default" position, dry specimens with the antennae oriented similarly can serve as a reference to determine which surfaces of the antennae bear describable features. In *Tmesibasis*, near the wing base, the surface between the anterior surface and the dorsal surface, or "anterodorsal" surface, bears a fringe of verticels. Similarly, the "posteroventral" surface also bears a verticel fringe. Most species exhibit darkened surfaces on the posterior surface of the flagellum near the eye (this consistently posterior darkening is also useful for distinguishing "correct" orientation of the various surfaces).

Tmesibasis species have long drawn attention for the length of their antennae (Hagen 1862), which often exceed the length of the wings, particularly in males. The antennal length of each species is recorded in A2 Excel File 2 and discussed in the 'Cladistic analysis', character 2, below.

One subtle feature of the antennae, which is also found in *Allocormodes*, is the <u>setitori</u>. These are usually present in males, but only sometimes present in females, in species that have them. As opposed to those found in *Allocormodes*, which, in dorsal view, are more round basally and radially symmetrical, the setitori in *Tmesibasis* tend to be broader basally, somewhat crescent-shaped, and laterally symmetrical. In lateral view they are pimple-like, as in *Allocormodes*. Sometimes the apical margin of the setitorus is darkly pigmented.

Thorax

Cervical sclerite. In other Ascalaphidae genera the cervical sclerites are often evenly rounded apically and only narrowly flattened dorsally, and the surface is evenly covered in a fine but conspicuous texture of microtrichia. In many *Tmesibasis* species, the apex is slightly more broadly flattened dorsally and carinate along the margin of the flattened dorsal surface. Most of the surface bears visible microtrichia, but the surface just ventrad of the carina near the apex of the sclerite often has a narrow band of smooth texture and is differentially colored.

Velvety spots (A2 Figs. 7–11). One of the most distinctive features of the notum, the velvety spots are large, approximately round, distinctly dark, and often surrounded by a thin diffuse ring of yellow or pale brown color. In *Tmesibasis*, the largest spots on the mesoscutum (A2 Fig. 7) are accompanied by spots situated laterally on the pronotum medial transverse band, pronotum posterior flange, and mesoprescutum. Collectively these spots form a broad oblique stripe running along the owlfly’s ‘shoulder’ (A2 Fig. 10).

The spots are composed of densely aggregated dark microtrichia. A scraping of the surface of a spot placed in glycerin and visualized at 400x under a compound microscope reveals hundreds of short, stout, very dark, spicule-like trichia (A2 Fig. 10a–c). In fact, much of the entire surface of the integument of *Tmesibasis* (and many owlflies) is covered in fine microtrichia, and together with (or in contrast to) the underlying pigment, they render the surface in various tones. The microtrichia provide the sheen often seen on convexly curving surfaces, such as the vertex and notal lobes, and cause the change in color witnessed as a specimen is turned under a light source. They also causes some difficulty in describing integument coloration (gold? brown? golden brown?). The velvety spots, then, appear to be a special modification of the plesiomorphic microtrichial vestiture of the dorsum, but adapted to be dark in color. The function of the spots is unknown, but they may serve in species recognition and/or courtship displays. Alternatively, they may provide increased surface area for the dispersion of volatiles (pheromones, etc.) released at the integument surface, but thus far no glandular openings have been discovered, and other Ascalaphidae without the velvety spots also have dense microtrichia. There does seem to be some intraspecific variation in spot/border size, shape, and color. Further studies (SEM, histological sectioning, chemical assays, etc.) are needed to evaluate the external and internal anatomy of the spots to further formulate and test hypotheses regarding their function(s).

The velvety spots on the metascutum are not as dark in color as those on the pro- and mesothorax, and they lack the paler margins. They appear to have primarily a physical function as the anchor points for the apices of the anal processes when the wings are folded over the back. The ventral surface of the anal process bears a small dense patch of fine microtrichia that gain purchase on the corresponding microtrichia of the corresponding metascutal spot when the two surfaces are brought into contact (see discussion and figures in Tjeder 1992).

<u>Setae color</u>. External body setae in *Tmesibasis* are abundant and diverse, and it can be challenging to accurately characterize the color of any specific seta or setal group, particularly those that are in the yellow to dark brown range. Characterization of setae is often complicated by apparent color changes with changes in the angle of incident light. Setae often appear dark in shadow, then take on a high reflectance in direct light. Thus, some setae are described in this work variably, for example, “golden to dark brown” or “brownish yellow to golden brown”. Most commonly this occurs with setae that appear brown in shadow or diffuse ambient light, but that gradually become golden brown or golden when reflecting light from a directed source. Descriptions here attempt to include the range of apparent colors visible under standard viewing conditions (e.g., through a microscope lit by a fiber-optic light source) with different angles and intensity of lighting.

Legs

Femur, dorsoapical process* (A2 Figs. 12–15, *fdp*). The distal margins of the dorsal surface of the meso- and metathoracic (and to a lesser degree on the prothoracic) femora are drawn into a projection in many *Tmesibasis* species, becoming long and triangular in some. Often the ventral surface is colored brightly yellow, particularly in those species with the projection well-developed.

Tibia, upper fascia* (A2 Fig. 14, *tuf*). In several species of *Tmesibasis*, as well as in many other owlfly genera, there occurs on the dorsal surface of the tibia a feature observed as a short transverse fascia or very weak swelling. This line is situated at a point approximately two-fifths the total tibia length from its proximal end and only appears on the outside surface of the leg. It is expressed in many ways; sometimes it appears as a dark line of pigment, and other times as an abrupt transition from one integument color to another, for example from yellow to reddish brown. The line itself, or often the tibia surface distad of the line, sometimes appears to swell slightly or sit at a very slightly higher elevation, and the integument proximad of the line or swelling is often glabrous, whereas that distad of the line is fully setose. The line pigment also sometimes appears to penetrate the integument deeply as if it corresponds with an internal phragma, but examinations of macerated legs in *T. lacerata* reveal no such internal feature, although in *Allocormodes nigristigma* the lateral-most parts of the line do appear to co-occur with a slight thickening or sclerotization of the integument. There do not appear to be any pores or setal fringes associated with the line in *Tmesibasis*. The fascia could represent an external indication of an internal chordotonal organ, as found in the base of the tibia of many Neuropterida (e.g., Chrysopidae—see Miller 1970, 1984), but more careful analysis is needed to determine this.

Tibia, basidorsal pores* (A2 Fig. 15, *tbp*). Distal to the femur-tibia joint on the dorsal surface of the tibia occurs a pair of sublateral pores, similar in size to a seta socket, but not associated with setae in any specimen. These are occasionally marked by pigment, but are often inconspicuous. In macerated specimens they can be seen as sclerotized tubes or channels penetrating through the integument to exit on the inner surface of the tibia in or very near the tissues of the femur-tibia joint. They may be campaniform sensillae, but more investigation is needed in order to determine this.

Pretarsal claw (A2 Fig. 16). The ventral surface is bicarinate, with an axial carina running along each ventrolateral margin, these converging at the apex of the claw; each carina is studded with a single line of minute, closely spaced bumps (not serrations), with perhaps 25+ bumps along each carina.

Wings

Length. In the formal descriptions wing length is measured from the base of the axillary sclerites to the wingtip, in spread or unspread specimens; this is simply referred to as the length. Sometimes the wings are also described in terms of their "relative" lengths, which usually regards how the wingtips appear in relation to one another, for example when the hind wing appears to be longer than the forewing in unspread specimens.

Shape (A2 Fig. 21–24, 27–28). Wing shape is one of the most conspicuous features of the genus, and is characterized here by six metrics: (1) width of the wing base; (2) dimensions of the anal process (A2 Figs. 27–28); (3) ratio of wing width near at its midpoint (where it is widest) to its overall length; (4) degree of falcation (extent of subapical concavity of the posterior wing margin); (5) breadth and marginal curvature of the apical area; and (6) angularity of the wing apex.

The wing bases are strongly narrowed in both sexes. In Odonata, wing narrowing corresponds with an increased ability to turn sharply, improving maneuverability; however, it does not increase speed, and actually reduces the range of speeds available in flight; petiolate wings are thus advantageous for lower powered flight and hovering, and may be useful for courtship displays (all Wootton and Newman 2008). In Ascalaphidae, wing base narrowing seems to be a convergent derivation within several clades at both tribal and generic levels, but is relatively more common in the Haplogleniinae (unpublished data).

The anal process (A2 Figs. 27–28) is elongate and very narrow and, in most species, apically acuminate. Amongst African Haplogleniinae, *Tmesibasis* is one of only a handful of genera in which the process has this extreme shape, although nearly all of these genera display some degree of wing base narrowing, and corresponding process elongation and narrowing.

Wing width at mid-wing varies highly among the species, with wings of some species having a shorter broader profile, and others being more narrow (A2 Excel File 2, Figs. 21–24).

Wings of a few species are more falcate than in others. Females have larger and more falcate wings than males. Female wings also have broader <u>apical areas</u> than those of males.

The outline of the apical margin of the wing transitions to the wing posterior margin at an angle, but this inflection does not always occur at the true apex of the wing (i.e, the most distant point from the wing base—see for example Fig. 21, F_1). Rather, it occurs in a posterodistal position on the apical margin. For this reason it is here termed the <u>apical angle</u>*. A few species have rounded wing apices.

<u>Venation</u> (A2 Fig. 17–19). Major veins of the wing follow the typical pattern for owlflies (see also chapter 1, A1 Fig. 22). Veinlets and crossveins, however, are often highly irregular, particularly in the costal area, at the wing base, in the portion of the

radial area subtending R, and in the triangles. This irregularity is characterized by the bunching, forking, bending, and multiplication of crossveins.

There are some venational differences relative to genera with less derived wings (e.g., *Allocormodes*) in the cubital and anal veins as a result of wing narrowing, particularly secondary vein fusions with each other and with the posterior wing margin, as detailed in the formal descriptions.

The secondary fork of Rs_1 branches from Rs_1 obliquely and thus is easier to interpret than in *Allocormodes*, in which it is abrupt and resembles a crossvein (chapter 1, A1 Figs. 22, 26).

Areas (A2 Fig. 20). *Tmesibasis* wings express nearly all of the same areas as the putatively more primitive genus *Allocormodes* (chapter 1); only the compressed marginal domains are absent. As a result of wing base narrowing there is some reduction in the size of (1) the anal area (the cells are reduced to a single row), (2) the distal domains of the triangles (usually not developed, especially in the HW, or restricted to one or two cells), and (3) the cubital (FW) and posterior medial (HW) areas (reduced in overall surface area).

Pterostigma. The pterostigma, while present and discrete, is unremarkable in appearance and is characterized by its lack of conspicuous color, rather than a significant darkening as in other genera. It comprises few veinlets, but these are long. The cells between the veinlets bear some very diffuse cream pigment, often only expressed as mesal opacity, and are occasionally flecked with diffuse brown pigment as well. The margins of the pterostigma are formed by brown pigment in the flanking cells, as detailed in the genus and species descriptions.

Maculation (A2 Fig. 25). Along with wing shape, the charismatic maculation patterns of the wings are probably the most conspicuous feature of the genus. The patterns are formed by large areas of pigment extending from the margins of the wing into the interior. In evaluating the species it became necessary to develop a conceptual framework and nomenclature for the distribution and expression of the major areas of pigment. These have been generally termed 'blotches', and are as follows. Anterior blotch*: this refers to the band of pigment subtending vein R and extending from the wing base to the apical area; it fuses with the basal and apical blotches. Apical blotch*: comprises all the pigment occurring within the apical area (see chapter 1 for a definition of the apical area). Basal blotch*: includes all pigment posterad of Mp/Mp_1 at the base of the wing. Posterior mesal blotch*: positioned along the midpoint of the posterior wing margin; this more-or-less triangular blotch is highly variable in size and shape and as such is diagnostic for several of the species; it is often larger in females. Posterior subapical blotch*: this blotch rests between the mesal blotch and the apical blotch, and may be contiguous with them or separated from them, and its shape is also diagnostic for several species; in one species (*Tmesibasis larseni* Hölzel) it is broken into two pieces.

In a few species, the pigmented membranes of the wing blotches mesally are thickened and granular, and this granularity often takes on a dark red or brown tint.

Membrane coloration. In most males, the hyaline membranes of the wings, at least in the basal half, are tinted brown. In some males these membranes are nearly completely tinted. Males of two species, however, lack such pigment. In a single observed female (*Tmesibasis waelbroecki* van der Weele: JRJ_01238) the wing membranes are also very slightly tinted.

Blyzocyte* (A2 Fig. 26). Imbedded along the anterior blotch are several large cells (or groups of cells) that are nearly always devoid of pigment in their centers, being only margined on the anterior and lateral (and sometimes also posterior) margins. The portion of the membrane that lacks pigment forms a rounded shape, and these cells with their pigment voids are here termed blyzocytes (blyzo [Greek] 'bubble' + kytos [Greek] 'cell') or blyzocyte sets (for a group of blyzocytes), due to their appearance as (mostly) clear spaces, or bubbles, that contrast with the darkly pigmented ground. Typically the blyzocytes are slightly enlarged relative to the surrounding cells.

The blyzocytes and blyzocyte sets are numbered, starting at one (or zero), consecutively from the base of the wing to the apex. The first consistently expressed blyzocyte, termed 'bc1'*, sits between R and Mp proximal to the Rs fork. In several species, a blyzocyte or blyzocyte set proximad of bc1 also sits between R and Mp and is termed 'bc0'*; in at least one species (*Tmesibasis alberti* Navás) it is consistently filled with pigment. The next blyzocyte (or blyzocyte set) after bc1, ‘bc2’*, sits between R and Rs and usually comprises a single cell. The remaining blyzocytes all occur in sets (except occasionally when they are adventitiously reduced), ‘bc3’*, ‘bc4’*, and ‘bc5’*, and subtend R. The number of blyzocytes in each set is variable among (and to a lesser degree within) species, and the approximate count can be useful in characterizing a species. In species descriptions, a letter is placed at the end of each blyzocyte set designation (e.g, ‘bc5e’) to indicate the highest observed count of cells in the blyzocyte set.

There are also cells in the basal blotch that exhibit characteristics similar to the blyzocytes (margined only, centrally devoid of pigment), but inconsistently so. Thus they are not referred to as blyzocytes here and are described on an ad hoc basis in the species descriptions.

Cubital and medial triangles. The triangles do not differ substantially in shape or size from *Allocormodes*, but have the prefork areas with numerous, sometimes irregular, crossveins, and somewhat more reduced distal domains. The shapes of the distal domains are not diagnostic for species. At the terminus of the distal domains, however, there is, very commonly, an additional subtending cell or two. These vary somewhat in shape and position, and in some cases appear as extensions of the distal domain extending to the posterior wing margin. These additional subtending cells are termed the paramarginal cells* (A2 Fig. 20). Because they are inconsistently shaped and positioned, they are not considered structural elements of the distal domain proper. In some other genera they are more regular, giving the impression that they do belong to the distal domain, but that is here considered to represent a derived state. In some *Tmesibasis* specimens the presence of paramarginal cells is ambiguous; when this occurs, Cua_2 (FW) or Mp_{2p} (HW) may continue in a straight line to the posterior wing margin, or, more commonly, it may terminate in a marginal cell or cells.

Abdomen

Microtrichia. As with the rest of the body, many abdominal surfaces are obscured by golden or gray microtrichia. This is more conspicuous on some of the darker surfaces.

Tergum. The first tergite is sagitally divided into lateral plates (T1 plates) that are normal and unproduced. The remaining tergites are also unproduced in both sexes, and no specialized patches of setae occur. The dorsal pattern of the abdomen, however, is developed, and in most species is at least somewhat conspicuous. Photographs of live females (e.g., A2 Figs. 29, 30) show that the prominence of the pattern can be quite dramatic in life.

Sternum. The ventral surface of the abdomen is simple, lacks any secondary structure, and is uncomplicated in its colors and patterning. It is mostly brown, but many species have large, paired, diffuse yellow maculae on S3 (and sometimes also S4 and S5), and brown spots at the bases of its setae.

S2 acrosternite arms*. The S2 acrosternite is reduced to a pair of narrow, oblique, anterolateral arms.

Terminalia

In both sexes the ectoprocts are sometimes produced dorsally and somewhat bulbous.

Males (A2 Figs. 31, 33). Among African Haplogleniinae, the genitalia of male *Tmesibasis* most strongly resemble those of *Melambrotus* McLachlan, and to a lesser extent *Paramelambrotus* Tjeder and *Neomelambrotus* van der Weele. Specifically, the dorsally-situated gonarcus is simple and shallowly domed; the ventrally arranged parameres are entire, unprotruding, convex plates with longitudinally converging grooves, these plates form the ventral half of the acorn-shaped gonarcus-paramere complex (GPC); where the paramere faces meet ventromedially, they form a narrow spindle-shaped groove, inside which rests the similarly spindle-shaped pelta.

Females (A2 Figs. 32, 34–36). Most structures (e.g., distivalvae, ventrovalvae) are similar to those found in other owlflies, but differ in that the interdental space is well-defined between the ventrovalvae; the ligula is somewhat reduced, membranous, transversely weakly bilobed, and only weakly robust; and the interdens is reduced to a small, sagitally-oriented, blade-like tab emerging from a small sclerotized plate (the interdental plate*).

Larval morphology

The larvae of *Tmesibasis* are unknown.

The larvae that Withycombe (1923, 1925) describes as having dark bodies and white scale-like setae are *Allocormodes* and not *Tmesibasis* as he suggested and others have cited (i.e, Henry 1976). See chapter 1 for a discussion of Withycombe's mistaken identification.

Cladistic analysis

Overview

A phylogenetic analysis of the species of *Tmesibasis* based on morphological characters was performed in order to better understand evolutionary relationships among the species.

Character selection and data analysis

All ten species of *Tmesibasis* were included in this study. Specimens made available for the revisionary study were examined thoroughly and evaluated for conserved and potentially informative characters. Attention was paid particularly to those features that appear to be unique to or derived within the genus, constant among at least a few species, and more-or-less unambiguous in their expression and, therefore, satisfactorily quantifiable. These characters were interpreted as potentially of phylogenetic value, and were documented, described, scored, and analyzed.

An effort was made to characterize features from all major anatomical systems typically recognized and treated in Neuropterida. During the exploratory phase of character examination several iterations of character description and analysis were undertaken. Characters deemed to perform poorly (contribute more noise than signal) were removed. Thirty-nine characters of the head, thorax, wings, legs, and abdomen were ultimately included in the analysis. These are provided in the character matrix (A2 Table 1) and in list format below (see 'Characters').

Although all major body regions yielded useful characters, the greatest number of features discovered and scored was in the wings, and included shape ratios, cell attributes, blotch pattern shapes and distributions, and wing pigment granularity. Most characters were binary, but a few were scored for more states, up to seven. Several characters were sex-specific.

Computational methods

Analyses were performed in TNT (Goloboff et al. 2008), using implicit enumeration with default settings. No characters were designated as additive (although the putative plesiomorphic state was coded as 0 and derived states as 1, 2, etc.), or otherwise weighted. The analysis was rerun in PAUP* (Swofford 2002), as a branch and bound parsimony search using defaults settings. Bremer supports were calculated in PAUP* using TreeRot (Sorenson 1999). The consistency index (C. I.) retention index (R. I.), and other statistical measures were generated in PAUP*, as were lists of taxon synapomorphies by branch (A2 Table 2) and character state changes by character (A2 Table 3).

Outgroup selection

No higher-level phylogenetic analysis has been published for haplogleniine owlflies. In order to polarize the cladistic analysis, an outgroup taxon was sought that exhibited the greatest number of similarities to the ingroup while still falling confidently outside the ingroup. At first glance this is a particular challenge—*Tmesibasis* seems to be among the most derived genera in the Haplogleniinae. Its long antennae, distinctive wing shape and striking wing patterning set it apart from all other haplogleniinae genera and obscure its relationships within the subfamily.

However, some other aspects of its morphology suggest a relation to several of the African genera. Chief of these is the simplified male genitalia, particularly the GPC. Among African Haplogleniinae, the genitalia of male *Tmesibasis* most strongly resemble those of *Melambrotus* and *Paramelambrotus*, and to a lesser extent *Neomelambrotus* (see Tjeder 1992). In these genera, the GPC has a simple, shallowly-domed, gonarcus. The parameres are entire, not-protruding, convex plates that form the ventral half of the GPC. The parameres bear longitudinal grooves, and medially between them is a narrow, spindle-shaped gap, within which sits the pelta. In other genera of African Haplogleniinae the GPC is more elongate, and the parameres are produced and protrude from the GPC ventrad or laterad (all interpreted to be derived conditions).

Among *Melambrotus*, *Paramelambrotus*, and *Neomelambrotus*, the last genus expresses the fewest similarities to *Tmesibasis*. In *Neomelambrotus* the body and wings are smaller, the thorax is much more pilose, the abdomen bears distinctive tufts of setae, and the parameres of the GPC are more heavily grooved. *Melambrotus* and *Paramelambrotus* are more similar to *Tmesibasis* in body size, pilosity, and paramere structure. In *Paramelambrotus*, the wing bases are distinctly less narrowed than in *Tmesibasis* and the abdomen is must more setose. *Paramelambrotus*, however, is monobasic, being known from only a single specimen that was not available for this study. In *Melambrotus*, the wing bases are more narrowed and the abdomen pilosity is more sparse, similar to that of *Tmesibasis*, and many specimens were available for this study. *Melambrotus* was selected as one outgroup taxon.

One characteristic of TNT (and other parsimony) analysis is that it cannot recover a unique character optimization or Bremer supports on the basal-most node of a topology. In order to enable the recovery of genus-level synapomorphies and node support for *Tmesibasis*, a minimum of two outgroups were needed. *Allocormodes* was selected as the second outgroup. *Allocormodes* is inferred to be among the most basal of haplogleniine owlflies in Africa on the basis of its unreduced wing bases, the condition of narrowed wing bases being found in all other African genera (except *Paramelambrotus*). Narrowed wing bases, particularly of the forewing, consistently occur as a derived feature in the Ascalaphidae, as demonstrated in recent phylogenies of *Allocormodes* (chapter 1), the Haplogleniinae of the Western Hemisphere (chapter 3) and the entire Ascalaphidae (chapter 4).

Characters

Head

[1] Vertex, lateral and mesal plates

    0 present, well-developed, distinct (chapter 1, Fig. 5, *mp*, *lp*)

1 absent, or very poorly developed, indistinct

Post-analysis comments: The presence of distinct plates is a feature of the vertex of *Allocormodes* (see chapter 1, Fig. 5, *mp*, *lp*) and is also seen in *Melambrotus*. In *Tmesibasis* the plates are completely lost or very weakly expressed in all species.

[2] Eye, posteromesal transverse depression

0 absent (Fig. 2)

1 present (Fig. 3)

Post-analysis discussion: Several distally placed species of *Tmesibasis* were discovered to exhibit subtly divided eyes. Divided eyes, however, are the synapomorphy for the subfamily Ascalaphinae. But amongst members of that subfamily, the dividing sulcus is not uniformly expressed, and in some genera is weak and appears merely as a depression (e.g., *Fillus*). Conversely, at least one genus with weakly divided eyes is known within the Haplogleniinae, *Proctolyra*. *Proctolyra* has several features that suggest that its true phylogenetic position lies with some genera of the Ascalaphinae (primarily the greatly produced male ectoprocts, but also wing shape and venation). However, *Tmesibasis*, which shares many features in common with several African haplogleniine genera, fits firmly within the Haplogleniinae (chapter 4) as it is currently interpreted. The discovery of the transverse depression in several species of *Tmesibasis* adds further to a growing body of evidence that the division of the eye is an anatomically variable, phylogenetically dynamic, and likely convergent feature that may need reinterpretation as a synapomorphy of the Ascalaphinae. Future higher level phylogenetic analyses of the

Ascalaphidae should lead to a better understanding of the placement of apparent subfamilial misfits.

[3] Antennae length to FW length ratio, females

0 <1.03 (Fig. 74)

1 1.04-1.13

2 >1.14 (Fig. 66)

Pre-analysis comments: Antennae are consistently longer than the wings in males, and always longer of those of females in *Tmesibasis* species, but female antennal length was observed to vary among species. Some species exhibit antennae with lengths approximately co-equal to wing length (state 0), others have much longer antennae (state 2), and the remaining species have antennae of intermediate length (state 1). To correct for normal differences in body size, antennal length here is scaled to forewing length. Antennae length for the female of *T. larseni* was determined from Hölzel's (1983)original description and figure.

Post-analysis comments: Long antennae (state 2) occur in *T. imperatrix* and *T. majesta*. Short antennae (state 0) occur in *T. larseni*, *T. rothschildi*, and *T. waelbroecki*. The remaining species of *Tmesibasis* exhibit antennae of intermediate length (state 1). The outgroups all express short antennae.

[4] Antennal apex, shape

0 club well-formed, distinct from more proximal portion of flagellum, width of widest club flagellomere ca. 2x its length (A2 Fig. 4)

1 club ill-formed, distinction from more proximal portion of flagellum ambiguous, width of widest "club" flagellomere ca. co-equal to or much less than its length (A2 Figs. 5, 6)

Post-analysis comments: Only two species of *Tmesibasis*, the phylogenetically basal *T. larseni* and *T. rothschildi*, have what may be considered a well-formed club. Loss of the club, and perhaps lengthening of the overall antennae, seem to correlate with the lengthening and narrowing of individual flagellomeres comprising the club; in the species with moderately well-formed clubs have very short wide club antennomeres, whereas in the most derived species, the width of nearly all club antennomeres has become co-equal with that of remaining flagellomeres, and considerably lengthened.

[5] Antennal coloration, basiposterior surface

0 concolorous with other basal surfaces of antennae

1 darkened on first 5–6 flagellomeres, but no more

2 darkened on first 7+ flagellomeres, and often along entire length, or nearly so, of flagellum

Post-analysis comments: State 2 is a synapomorphy for *T. majesta*.

[6] Antennal apex terminal flagellomeres, color

0 brown, not completely yellow (A2 Figs. 4, 5)

1 completely yellow (A2 Fig. 6)

Pre-analysis comments: The color of the antennal apex is very consistent from species to species, with a few exceptions, which appear to be adventitious, in a few individual specimens.

Post-analysis comments: Brown terminal flagellomeres (state 0) were observed in the more basally placed species *T. larseni*, *T. rothschildi*, *T. waelbroecki* and *T. simplex*. Yellow terminal flagellomeres (state 1) are a derived condition, occurring in the more distally placed *Tmesibasis* species.

Thorax

[7] Pronotum anterior flange lobes, medial coloration

0 medium brown, concolorous with dorsal surfaces on remainder of pronotum (A2 Fig. 8)

1 dark brown to black, darker than dorsal surfaces on remainder of pronotum (A2 Fig. 9)

Post-analysis comments: The pronotum anterior flange lobes are distinctly anteromedially darkened (state 1) in *T. alberti*, *T. lacerata* and *T. majesta*. Slight darkening was observed to occur adventitiously in a few specimens of a few other species.

Legs

[8] Dorsoapical process of meso- and metathoracic femora

0 short, only moderately acute (A2 Fig. 12, *fdp*)

1 long, acuminate (A2 Fig. 13–15, *fdp*)

Pre-analysis comments: In species with the process short, its shape in outline is somewhat rounded and its apex only moderately acute, and its length is much shorter than its width. In species with the femur dorsoapical process long (state 1), the process is triangular in outline and its length is approximately co-equal to its width. No function for the process, which is noted for the first time here, is known.

Post-analysis comments: The apical process of the femur (state 1) is very short in *T. larseni* and *T. rothschildi* (and outgroups), but long and well-developed in all other *Tmesibasis* species.

[9] Dorsoapical process of meso- and metathoracic femora, color

0 dull brownish yellow (A2 Fig. 12, *fdp*)

1 bright yellow (A2 Figs. 13, 14, *fdp*)

Pre-analysis comments: The color characterized here occurs on the ventral or inner surface of the process.

Post-analysis comments: Bright yellow processes occur in those species in which the process is also long and acuminate (character 6, state 1).

[10] FW length to FW width ratio, males

0 >4.47

1 3.77–4.40 (Fig. 23)

2 <3.68 (Figs. 21, 22)

Pre-analysis comments: Wings are long and very slender in the outgroups (state 0) and long and slender in a few of the ingroup species (state 1, Fig. 23). A small but distinct gap in ratios was observed between this group and the remaining species of *Tmesibasis* (A2 Excel file 2), which exhibit a range of ratios and corresponding wing shapes, from somewhat long and moderately slender to short and broad (all state 2, Figs. 21, 22).

Post-analysis comments: Long and slender wings (state 1) were observed in *T. imperatrix* and *T. majesta*.

[11] FW apex, shape, females

0 anterolateral margin unexpanded to only weakly expanded, apex of wing not produced distinctly distad of apical angle (e.g., A2 Fig. 24, F_2)

1 anterolateral margin expanded, apex of wing produced distinctly distad of apical angle (A2 Fig. 45)

Post-analysis comments: The anterolateral margin is produced (state 1) in females of *T. imperatrix*.

[12] FW apical angle, shape

0 rounded (A2 Figs. 21 [F_1], 23)

1 angulate (A2 Figs. 22, 24 [F_2])

Pre-analysis comments: See discussion regarding the apical angle under 'Wings/shape', in 'Adult morphology', above.

Post-analysis comments: Basal members of *Tmesibasis*, *T. larseni* and *T. rothschildi*, have rounded wing tips.

[13] FW anal margin

0 anal margin convex, without an acuminate process (A1 Fig. 26)

1 anal margin mesally concave, with an acuminate process (A2 Fig. 23, *B*)

Post-analysis comments: An acuminate anal process (state 1) is present in all species of *Tmesibasis* and *Melambrotus*. In *Allocormodes*, the process is undeveloped in most species (see chapter 1).

[14] HW shape of posterodistal margin, males

0 convex

1 at least slightly concave, i.e, falcate (A2 Fig. 22)

Pre-analysis comments: The ancestral state was interpreted to be convex (non-falcate) wings.

Post-analysis comments: All *Tmesibasis* species have at least very slightly falcate wings, although the falcation is very weakly expressed in some of the basally placed species (e.g., *T. larseni* and *T. rothschildi*).

[15] Wing venation, density

0 dense, FW cubital area with ca. 10 more-or-less complete cells rows meeting wing posterior margin (A2 Fig. 89)

1 open, FW cubital area with ca. 7–8 more-or-less complete cells rows meeting wing posterior margin (A2 Fig. 93)

Post-analysis comments: Open wing venation (state 1) is an autapomorphy for *T. simplex*.

[16] Subcostal veinlets

0 more-or-less regularly spaced, simple, without crossveins, but one or two sometimes bunched or forked (A2 Fig. 99) at any point within costal area

1 mostly regularly spaced, but three or more conspicuously irregular in both distribution and form, forked or twigged, convergent and/or divergent, and/or connected by uneven crossveins, usually (but not only) in apical half of costal area (A2 Fig. 98)

Pre-analysis comments: Irregularity in the subcostal veinlets (state 1) was interpreted, pre-analysis, to be the derived state.

Post-analysis comments: State 1 was recovered as a plesiomorphic feature within the ingroup, being observed only in the basal-most species, *T. larseni*, *T. rothschildi*, and *T. waelbroecki*.

[17] Blyzocytes

0 absent (A1 Figs. 111, 112)

1 present (A2 Fig. 26)

Post-analysis comments: Blyzocytes are only found in *Tmesibasis* species; they are absent (state 0) in all outgroups.

[18] Anal process terminal cell shape

0 anal process undeveloped

1 anal process developed, membrane extending to near apex of process (A2 Fig. 27)

2 anal process developed, membrane terminating well before apex of process (A2 Fig. 28)

Post-analysis comments: Although the anal process is elongate and narrow in all *Tmesibasis* species, the terminal cell penetrates well into the process, and the sides of the process (=marginal vein C) remain separate and distinct from one another, in *T. larseni* and *T. rothschildi* (state 0). In species expressing the more derived state (state 1), the process becomes very narrow and apically acuminate, and the marginal veins on each side of the process approach one another until they fuse, crowding out the terminal cell posteriorly.

[19] FW and HW color pattern, reddish-brown marginal blotches

0 absent (A1 Figs. 111, 112)

1 present (A2 Fig. 25)

Post-analysis comments: The pattern of reddish-brown blotches is a synapomorphy for the genus. The pattern is least developed in the basal-most species of *Tmesibasis*, *T. larseni*, but is most well-developed in *T. waelbroecki*, the basal-most species in the largest and most well-defined clade within the genus.

[20] Subcostal area, pigment

0 absent

1 present, even

2 present, but with gaps corresponding to costal area cells

Post-analysis comments: State 2 was observed only in *Tmesibasis*.

[21] Blyzocytes 0, 1 and 2, pigment, males

0 at least center of cell broadly devoid of pigment

1 cell completely or nearly completely pigmented (A2 Figs. 37)

Post-analysis comments: Completely, or nearly completely, pigmented blyzocytes 1–3 (state 1) are an autapomorphy for *T. alberti*.

[22] FW mesal blotch height, males

0 blotch absent

1 blotch present, moderately tall to tall, height one-third to approximately coequal width along wing posterior margin (e.g., A2 Figs. 51, 92)

2 blotch present, short, height approximately one-fourth width along wing posterior margin (A2 Fig. 88)

Post-analysis comments: The very short mesal blotch (state 2) is a synapomorphy for *T. scopsi*.

[23] FW mesal blotch anterior margin, outline shape, males

0 blotch absent

1 blotch present, anterior margin entire, acute, not elongate or curved (A2 Fig. 46)

2 blotch present, medial portion offset from basal portion, broad, elongate, and often curved proximad (A2 Fig. 68)

Post-analysis comments: The mesal blotch is secondarily produced (state 2) in *T. majesta*.

[24] FW subapical blotch pigment, shape, males

0 absent

1 present, very short, most-produced anterad on proximal and distal margins of blotch and unproduced mesally, often separated into two small marginal blotches (A2 Figs. 59, 73, 75, 76)

2 present, very short, most-produced anterad mesally, thinly connected to apical blotch but separated from mesal blotch (A2 Figs. 44, 65)

3 present, moderately short, most-produced anterad mesally, thinly connected to both apical blotch and mesal blotch (A2 Figs. 81, 88, 92)

4 present, moderately short, most-produced anterad mesally, separated from apical blotch in radial area (not apical area) by a complete gap in pigment, sometimes thinly connected to mesal blotch (A2 Fig. 37)

5 present, tall, most-produced anterad mesally, often separated from both apical and mesal blotches by a gap in pigment (A2 Fig. 51)

6 present, moderately tall, most-produced anterad mesally, broadly connected to both apical and mesal blotch (A2 Fig. 96)

Pre-analysis comments: The expression of the subapical blotch is essentially consistent in both wings but, for simplicity, was coded only for the FW.

Post-analysis comments: The expression of the subapical blotch is both diagnostic and phylogenetically informative for *Tmesibasis* species, with one state (2) recovered as a synapomorphy for one species group (node 8). State 1 was observed in *T. larseni* and *T. rothschildi*. State 2 unites *T. imperatrix* and *T. majesta*. State 3 was observed in *T. royi*, *T. scopsi*, and *T. simplex*. States 4–6 were observed only in *T. alberti*, *T. lacerata*, and *T. waelbroecki*, respectively.

[25] FW apical blotch pigment, distribution, males

0 absent (A1 Fig. 111)

1 present, but absent along posterior wing margin in apical area (A2 Fig. 61)

2 present, complete along posterior wing margin in apical area (A2 Fig. 54)

Pre-analysis comments: For the purposes of this character, the apical blotch pigment was interpreted to be that pigment which is confined to the apical area (although in several species, the pigment bleeds into the radial area along Sc+R).

Post-analysis comments: All outgroup species lack apical blotch pigment, while all ingroup species possess it. Within the ingroup, state 2 occurs in *T. larseni* and *T. rothschildi*.

[26] FW apical blotch mesal cells pigment voids, males

0 absent

1 present, mesal margins of at least three or four adjoining cells devoid of pigment where they join (e.g, A2 Fig. 54)

2 present, mesal margins of adjoining cells margined where they join, mesal cells with voids aligned (A2 Figs. 61, 73, 75)

3 present, mesal margins of adjoining cells margined, mesal cells with voids unaligned (A2 Fig. 37)

Post-analysis comments: State 3 is an autapomorphy for *T.alberti*.

[27] Blotches, cell membrane pigment, mesal granularity

0 absent

1 present, often coarse (A2 Fig. 62)

Pre-analysis comments: This granularity, which has a distinct appearance, is imbedded in the pigment that lies in a thin layer between the dorsal and ventral surface layers of the cell membranes. It occurs in membranes of all blotch areas of the wing in a few species.

Post-analysis comments: Coarse granularity in cell pigmentation is observed in *T. larseni* and *T. rothschildi*.

[28] FW membranes, hyaline area pigmentation, males

0 absent, lacking pigment completely (A2 Figs. 44, 65)

1 present, darkly tinted reddish brown evenly throughout wing (A2 Figs. 59, 73, 92, 96)

2 present, lightly tinted reddish brown only in basal half to two-thirds of wing, fading to absent in distal half to on-third of wing (A2 Figs. 37, 51, 81, 88)

Pre-analysis comments: "Hyaline areas" of the wing refer to the transparent, non-blotch-bearing regions, which, in many ingroup species, are tinted with reddish-brown color.

Post-analysis comments: Males with hyaline wing membranes completely tinted (state 1) is the plesiomorphic state for the genus; membrane tinting is secondarily lost completely (state 0) in *T. imperatrix* and *T. majesta*.

[29] HW mesal blotch shape, females

0 blotch absent

1 blotch present, anterior apex of pigment separated from posterior margin of anterior blotch by three rows of cells, apex strongly recurved proximad (toward wing base)(A2 Fig. 74; Hölzel 1983, fig. 2)

2 blotch present, anterior apex of pigment separated from posterior margin of anterior blotch by two rows of cells, apex not strongly recurved proximad (toward wing base)(A2 Figs. 38, 82, 97)

3 blotch present, anterior apex of pigment separated from posterior margin of anterior blotch by two rows of cells, apex recurved proximad (toward wing base)(A2 Figs. 45, 52, 66)

Post-analysis comments: State 1 was observed in *T. larseni* and *T. rothschildi*. State 2 was observed in *T. albert, T. royi* and *T. waelbroecki*. State 3 was observed in *T. lacerata*, *T. majesta*, and *T. imperatrix*. The shape of the blotch is unknown for *T. scopsi* and *T. simplex*, for which females are undescribed.

[30] HW subapical blotch pigment, shape, females

0 absent

1 present, very short, most-produced anterad on proximal and distal margins of blotch and unproduced mesally, not joined to mesal or apical blotches (A2 Figs. 60, 74)

2 present, moderately tall, most-produced anterad mesally, somewhat broadly connected to both mesal and apical blotches (A2 Fig. 97)

3 present, moderately tall, most-produced anterad mesally, not connected to mesal blotch, connected narrowly or not connected to apical blotch (A2 Figs. 38, 52)

4 present, at least moderately tall, most-produced anterad distally, connected narrowly or not connected to mesal blotch, broadly connected to apical blotch (A2 Figs. 45, 66, 82)

Pre-analysis comments: The expression of the subapical blotch varies slightly from the FW to the HW, but is more consistent among species in the HW.

Post-analysis comments: State 1 was observed in *T. larseni* and *T. rothschildi*. State 2 was observed only in *T. waelbroecki*. State 3 was observed in *T. alberti* and *T. lacerata*. State 4 was observed in *T. royi*, *T. majesta*, and *T. imperatrix*. The shape of the blotch is unknown for *T. scopsi* and *T. simplex*, for which females are undescribed.

Abdomen

[31] T1 plates, males

0 laterally pale, with dark spots marking setal bases distinct from ground color

1 completely very dark cinnamon brown, with dark spots marking setal bases blending into ground color (A2 Fig. 83, T1)

Post-analysis comments: Completely dark T1 plates were observed in *T. royi* and *T. simplex*.

[32] T1 mesal membrane, males

0 anteriorly smooth, non-carinate

1 anteriorly puckered, carinate (A2 Fig. 83, see arrow)

Post-analysis comments: Membrane puckering (state 1) is a synapomorphy for *T. royi*.

[33] T3, posterolateral maculae

0 absent

1 present as small spots along posterior margin of tergite

2 present as large, dark, triangular marks (Figs. 29, 30)

Post-analysis comments: Almost all species of *Tmesibasis* have distinctive posterolateral maculae on the abdominal tergites. In *T. larseni* the maculae more closely resembles those of *Melambrotus*, that is, posterior dark spots only (state 1).

[34] Setal spots

0 absent

1 present

Post-analysis comments: Setal spots are present on the abdominal tergum and sternum in *Melambrotus* and *Tmesibasis*.

[35] S3, posterolateral maculae

0 absent

1 present

Pre-analysis comments: Large, paired, diffuse yellow maculae occur on the posterolateral margins of S3 in some species in the analysis.

Post-analysis comments: *Melambrotus* shares the maculae with *Tmesibasis*, although the maculae are consistently dark brown in *Melambrotus*. They are yellow to dark brown in *Tmesibasis*.

[36] GPC, basal width, ventral view

0 narrow (Figs. 64, 78)

1 broad (e.g., Figs. 41, 70, 85)

Post-analysis comments: A narrow GPC base was observed in the outgroups and in *T. larseni*, *T. rothschildi*, and *T. waelbroecki*.

[37] GPC, dorsal margin outline, lateral view

0 entire, convex

1 subapically very slightly concave (Figs. 84, 94)

Post-analysis comments: State 1 was observed in *T. simplex* and *T. royi*.

[38] Interdens, width of base, lateral view

0 very thin (interdens transverse, lateral view = cross-section)

1 very narrow (interdens a cone-like pin; see Tjeder 1992: fig. 211, *id*)

2 narrow (A2 Fig. 80)

3 moderately narrow (A2 Fig. 87)

4 wide (e.g., A2 Fig. 50)

Pre-analysis comments: In *Allocormodes*, the interdens is a tab that lies transverse or perpendicular to the body axis (state 0). In *Melambrotus* the interdens is a narrow, radially symmetrical pin (state 1). In the ingroup the interdens is an elongate blade of various sizes whose axis lies along the sagittal line.

Post-analysis comments: State 2 was observed in *T. rothschildi*. State 3 was observed in *T. royi*.

[39] Interdens, outline shape, lateral view

0 subrectangular, apex not secondarily narrowed (transverse)

1 acuminate, apex not secondarily narrowed (pin-like)

2 curved, apex not secondarily narrowed (e.g., A2 Figs. 58, 87)

3 subrectangular, apex not secondarily narrowed (A2 Fig. 103)

4 curved (at base), apex secondarily narrowed and subrectangular (A2 Fig. 72)

Post-analysis comments: State 3 is an autapomorphy for *T. waelbroecki*. State 4 is an autapomorphy for *T. majesta*.

Results

Taxonomic placements and support

Analysis in TNT and PAUP* resulted in a two similar most-parsimonious trees. Strict consensus of the trees (A2 Fig. 1) resulted in a tree with the basal relationships among ingroup species completely resolved, but the six remaining species placed distally in a single clade mostly unresolved (node 6), except for one species pair. The possible reasons for this lack of resolution will be discussed below. The attributes of the consensus tree will now be discussed.

The consensus tree (A2 Fig. 1) has the following statistical properties: length 76 steps; number of parsimony-informative characters: 28; consistency index (CI) = 0.8684; homoplasy index (HI) = 0.1316; CI excluding uninformative characters = 0.8246; HI excluding uninformative characters = 0.1754; retention index (RI) = 0.8507; rescaled consistency index (RC) = 0.7388.

Tmesibasis was recovered as monophyletic with very high Bremer support (A2 Fig. 1, node 2: 8). Eight unambiguous synapomorphies were found for this clade (see A2 Table 2 and the taxonomic treatment for genus *Tmesibasis*, below), including, as a few examples, the expression of the distinctive pattern of reddish-brown marginal blotches (char. 19, state 1), the presence of blyzocytes (char. 17, state 1), and the hind wing in males being at least slightly falcate (char. 14, state 1).

Tmesibasis larseni and *T. rothschildi* were placed together as sister taxa in a clade near the base of the genus (node 3: 1). Two unambiguous synapomorphies supported this relationship: the forewing apex in females produced distad of the apical angle (char. 11, state 1), and the cell membranes of the blotches with their pigment mesally granular (char. 27, state 1).

The remaining ingroup species were placed together in a single, large clade with high Bremer support (node 4: 6). This clade was supported by the following seven unambiguous synapomorphies: the presence of a posteromesal transverse depression in the eye (char 2, state 1); the loss of a well-formed antennal club (char. 4, state 1); the development of a long, acuminate, bright yellow, dorsoapical process of meso- and metathoracic femora (chars. 8, state 1, and 9, state 1); an angulate FW apical angle (char. 12, state 1); posterior reduction in cell membrane in the terminal cell of the anal process (char. 18, state 2); and the forewing apical blotch pigment complete along the posterior wing margin in the apical area (char. 25, state 1).

Within this large clade, two species (*T. waelbroecki*, *T. simplex*) were placed in a pectinate arrangement along the stem forming the base of the clade. The clade including *T. simplex* + remaining *Tmesibasis* (node 5: 1) was supported by a single synapomorphy, the base of the GPC broad (char. 36, state 1). The unresolved clade containing the remaining *Tmesibasis* species (node 6: 1) was supported by two synapomorphies: the antennal apex terminal flagellomeres completely yellow (char. 6, state 1); and the forewing membranes in males with the hyaline area darkly tinted reddish brown only in the basal half to two-thirds of the wing (char. 28, state 2). The sister group relationship between *T. imperatrix* and *T. majesta* had moderate Bremer support (node 7: 2) and was supported by five synapomorphies: long antennae in females (char. 3, state 2); long narrow wings in males (char. 10, state 1); the subapical blotch pigment in male forewings very short, thinly connected to the apical blotch but separated from the mesal blotch (char. 24, state 2); the forewing membranes in hyaline areas of males devoid of pigment (char. 28, state 0); and the HW mesal blotch in females with its anterior apex separated from the posterior margin of the anterior blotch by only two rows of cells, and the proximal margin recurved proximad (toward wing base) (char. 29, state 3).

The lack of resolution in the distal part of the tree results in part from conflict among a small number of phenotypic characters that might unite some of the most recently evolved species groups in *Tmesibasis* into species-groups (i.e., those species distad of node 6). Although *Tmesibasis* is character rich at the genus level, and at least one unambiguous synapomorphy was recovered in the analysis for nearly every species (only *T. larseni*, and *T. rothschildi*, each of which are readily diagnosable by their wing patterns and combinations of other features, were placed without synapomorphies), very few characters were discovered which supported groups of species for the distally placed taxa. The few that were discovered appear to have conflicted with one other, as they were not recovered as synapomorphies in the final character state optimizations.

Examination of the distributions of character states as optimized onto the tree and the placement of synapomorphies provide much insight into the direction of evolution of morphology across *Tmesibasis*. These changes will now be briefly discussed (see A2 Tables 2 and 3).

Review of character changes

Eye depression

The depression first arises in *T. waelbroecki* (char. 2, node 4), and is seen in all more derived ingroup species except *T. majesta*, in which it is secondarily lost.

Antennae

The plesiomorphic condition of the antennae within *Tmesibasis* is antennae with length approximately co-equal to wing length, with evenly brown coloration and with moderately well-developed clubs. In more derived species, the club first narrows and its component antennomeres elongate, and with them the entire antennae lengthens, especially in males (char. 4, node 4). In a few more derived species, the apical antennomeres are yellow (char. 6, node 6), and the antennae become as long in the females as in the males (char. 3, node 7).

Femur dorsoapical process

This feature (char. 8, state 1) is absent in basal species. It first appears in *T. waelbroecki*, and occurs in all species distad of node 4.

Wings: dimensions/shape

Plesiomorphic wing traits include shorter, broader wings (char. 10, state 2) that are not falcate (char. 14, state 0), with rounded apices (char. 12, state 0); also, the FW anal process is well-developed, elongate and narrow (char. 13, state 1). One of the first wing innovations within the genus was the development of a slight falcation in the wing apex (char. 14, state 1, node 2). Subsequently, the wing apical angles developed a sharp posterior point (char. 12, state 1, node 4), and a few species developed very long and narrow wings (char. 10, state 1, node 7).

Wings: veins and cells

Three basal species of *Tmesibasis* (*larseni*, *rothschildi*, *waelbroecki*) have highly irregular costal area venation, and it was anticipated pre-analysis that this feature might unite the species into a monophyletic clade, but that interpretation is not supported by character optimizations. The current analysis identifies irregular costal crossveins as plesiomorphic within *Tmesibasis* (char. 16, state 1, node 2), followed by the establishment of regular Sc veinlets (char. 16, state 0, node 5) similar to the condition observed in the outgroups. The highly conspicuous blyzocytes (char. 17) are also synapomorphic for *Tmesibasis* (node 2), and occur in all living species.

Wings: patterns

As with the blyzocytes, the distinctive pattern of cinnamon-colored triangles (char. 19, state 1, node 2) is found in all extant species of *Tmesibasis*. In the basal-most species, *larseni*, the pattern is very narrow along the wing margins and the ‘triangles’ are small (the subapical blotch is actually composed of two very small blotches somewhat distantly separated: char. 24, state 1). The pattern takes up more of the wing margin in *rothschildi* (in both *larseni* and *rothschildi*, there is distinct narrow channel in the apical area lacking pigment between the subapical and apical blotches: char. 25, state 1), and then fused into broad bands of dark pigment in *waelbroecki* (char. 24, state 6). In more derived species species (node 5), however, the pigment is not as broad along the posterior margin and the triangles become more-or-less consistent in size. Also (node 5), the sexes begin to differ dramatically in the size and shape of the triangles (compare chars. 23, 24 and 29, 30). More derived species express very slight but consistent differences in the size and shape of the triangles and in their proximity to one another, particularly in males (chars. 23, states 1, 2; char. 24, states 1–6).

In all *Tmesibasis* species, the subcostal area is filled with pigment (except for the gaps: char. 20, state 2), and in all but two species the wing membranes of males have a reddish brown tint (char. 28). The tint covers more of the wing in the basal species (char. 28, state 1, node 2), and gradually reduces (char. 28, state 3, node 6), until it is lost altogether in *majesta* and *imperatrix* (char. 28, state 0, node 7). In *larseni* and *rothschildi*, the darkly pigment areas (blotches) exhibit a granularity distributed mesally in the cells (char. 27, state 1, node 3).

Abdominal tergum: dorsolateral maculae

In *Melambrotus* (and in other owlfly genera), the posterolateral region of the abdominal tergite 3 (T3) and subsequent tergites bears a pair of small, very dark and distinct maculations. Most species of *Tmesibasis* have a large, well-developed, dark, subtriangular or quadrangular macula in this region (char. 33, state 2). In *larseni*, though, the macula is small and dark (char. 33, state 1), reminiscent of *Melambrotus*, and so they were coded identically. The maculation of *larseni*, however, is diffuse, and has the hint of the triangular shape that appears in the more derived species. It should be pointed out that this observation was of a single specimen of *larseni*, the only one available still retaining an unmacerated abdomen. This putative similarity will need to be corroborated through examinations of additional material.

Taxonomic treatments

Genus **Tmesibasis** *McLachlan, 1871*

Type species *Ascalaphus lacerata* Hagen, 1853

Tmesibasis McLachlan, 1871

—McLachlan 1871.09.14 r#353: 242 {TSP: *Ascalaphus lacerata* Hagen. TS: not explicitly indicated [holotype by explicit monotypy]. DIS, GD, OD, K.}

Etymology and nomenclatural notes.—unexplained, probably 'Tmesi–' (from Greek tmesis, cut) + 'basis' (from Latin basis [feminine], a foundation, or Greek basis [feminine], a stand, base, or a step whereupon one stands), in reference to the strongly petiolate wing bases. Gender: Feminine, from the gender of the Latin noun 'basis', Art. 30.1.1. Proposed common name: 'brown-blotched bladewings', in reference to the patterning and shape of the wings.

Diagnosis.—Antennae very long, subequal to considerably longer than the wings, with clubs poorly differentiated (weakly clavate to nearly filiform), elongate and narrow.

Thorax with large, black, round, or kidney bean-shaped, velvety spots. Wings with strongly narrowed bases, usually more-or-less falcate in apical third, and apices often acuminate; FW with a very well-developed and narrow anal process; wings bearing a distinctive pattern of cinnamon-brown marginal triangle-shaped maculae ("blotches"), hyaline membranes often with fuscous tint in males. Abdomen much shorter than the wings, tergites often dorsolaterally patterned with paired, elongate, dark, curved triangles.

Synapomorphies.—Vertex plates very poorly developed or lost (char. 1, state 1); wings at most only moderately slender (char. 10, state 2); HW in males at least slightly falcate (char. 14, state 1); blyzocytes present (char. 17, state 1); pattern of reddish-brown marginal blotches present (char. 19, state 1); FW mesal blotch in males with height one-third to approximately coequal width along wing posterior margin (char. 22, state 1); FW mesal blotch in males with anterior margin entire, acute, not elongate or curved (char. 1, state 1); FW membranes in males with hyaline area darkly tinted reddish brown evenly throughout wing (char. 1, state 1).

Description.—

Size (mm). Male: length of body 21–30, abdomen 14-21, forewing 24-33, hind wing 23-33, antennae 25-42. Female: length of body 20–30, abdomen 12-21, forewing 29-38, hind wing 28-40, antennae 30–46.

Head (A2 Figs. 2–6). Occiput smooth, glabrous. Postorbital sclerite thin, mostly even in width but sometimes broadening, glabrous. Vertex deeply bilobed, mesal surface of each lobe with granular texture of golden brown microtrichia and long wispy brown setae. Prefrons open and glabrous posteriorly. Anterior extra-torular sclerites well developed. Frons swollen, bearing moderately dense covering of long slender setae. Clypeus bearing medium long slender setae mesally or sublaterally, these continuing laterad and becoming longer, darker, and often denser. Labrum with numerous slender curved setae. Paraocular band sometimes glabrous, sometimes with a few short setae, sometimes with a fringe of medium long setae running from mandible to anterior tentorial pit. Anterior orbital sclerite thin and even in width, fused with paraocular band, discernible only by its color. Anterior tentorial pit a long, closed, dorso-ventral slit. Posterior genal triangle often glabrous, but sometimes bearing some short, slender, setae. Mandibles often translucent, with some medium length slender golden setae laterally. Maxillary stipes and palpomere 1 with very long slender setae, remaining palpomeres with apical whorls of short setae. Submentum, mentum and palpigers with long slender setae; labial palpi bearing numerous short slender setae; ligula ventrally glabrous. Eyes golden brown, usually very slightly dorsoventrally oblong, posteriorly often at least weakly bilobed. *Antennae.* Scape globose, bearing a dense coat of long setae. Pedicel offset posterolaterally, shorter than wide, orangish brown, distal margin a yellow or orange ring; base of anterior surface with a pit, this supertending an oblique sulcus on the anterior surface of the scape. Flagellum with 36-47 flagellomeres, including club, which is only somewhat distinct in a few species; approximately five to ten basal flagellomeres with many long slender dark brown verticils arranged in an anterior and posterior fringe; all flagellomeres bearing numerous short slender dark brown setae, these becoming denser toward and on club, setitori absent to somewhat well developed. Club, when developed, a somewhat broad spindle, otherwise, poorly distinguished from other flagellomeres and number of included flagellomeres unclear, cylindrical, with flagellomeres gradually shortening until length of apical two or three is near equal to their width; apical flagellomere with a minute but elongate acuminate apex.

Thorax (A2 Figs. 7–11). *Cervix*. Dorsal cervical plates round to ovoid, bearing long very slender setae. Cervical sclerite covered with appressed microtrichia, anterior surface bearing long wispy setae, dorsal margin carinate, often narrowly smooth and differentially colored immediately below carina. Ventral cervical plate usually difficult to see, oblong and narrow, bearing very long slender yellow setae. *Pronotum*. More developed than in other genera; approximately one-fourth to two-fifths length of mesonotum, setae in paler areas often with a small reddish brown spot at their base. Anterior flange well-developed, sagittally divided into two large sublateral rounded triangular lobes, surfaces bearing numerous very long and slender erect setae. Medial transverse band very short mesally, broadening laterally; lateral surface very dark brown, concolorous with mesonotal velvety spot, and with it forming a broad oblique longitudinal stripe, lateral surfaces with some long and slender erect setae; posterolateral knob bearing numerous long slender brown setae. Posterior flange narrow longitudinally, raised dorsally and laterally but not produced posteriorly, weakly divided medially by longitudinal sulcus; lateral surface greatly darkened with velvety spot texture as part of the oblique stripe; sublateral and lateral surfaces bearing numerous very long and slender erect setae. *Mesonotum*. Highly domed, elevated above wing bases and metathorax. Prescutum large, auriculate, width at anterior margin approximately coequal to sagittal length, anterolateral margins lobelike, deeply invaginated where they meet scutellum, posterior margin bordering scutum a weak depression; color brown, anterolateral lobes with dark brown velvety texture, participating in oblique velvety stripe; lobe surfaces bearing long and slender erect setae. Scutum narrow mesally, laterally forming large round lobes; color brown, mesal surface of each lobe bearing a velvety spot; surface with long and slender setae. Scutellum wider than long, round, dorsal elevation highest of thorax, posterior margin transversely swollen; color brown, posterior swelling bearing a narrow transverse yellowish stripe, surface posterad of stripe dark brown; lateral and posterior surfaces bearing long and slender setae. Subscutellum a narrow undeveloped band, glabrous. Postnotum sagitally divided into two lobes by a deep groove, glabrous. *Metanotum*. Paraprescutum a thin line or carina mesally, broadening laterally, small, distinct, glabrous. Prescutum short, glabrous. Scutum obliterate medially, lateral lobes broad and round, anterolateral surface with velvety spot texture, lateral and posterior surfaces bearing long and slender setae. Scutellum wider than long, mesally slightly depressed with posterior margin swollen transversely, lateral surface with a few long and slender setae. *Pleuron*. Mesanepimeron slightly produced at ventral margin of subalar membrane, forming a pimple-like projection. Pleurites more-or-less evenly brown; all surfaces bearing a dense coat of setae but this appearing sparse because setae long and very slender.

Legs (A2 Figs. 12–16). *Dimensions*. Legs moderately short. Coxae about half as long as femora. Trochanters about one-fifth to one-fourth femora length. Femora and tibia approximately co-equal in length; tibial spurs slightly variable in length, usually as long as first three tarsomeres, but sometimes as long as first four. Tarsomeres one to four collectively more-or-less co-equal in length to tarsomere five; claw also coequal in length to tarsomere five. *Morphology*. Dorsal surface of femur often prolonged apically into a triangular process overlapping femoral-tibial joint and base of tibia, but if so, then only somewhat elongate and acute on prothoracic femur, much longer and more acute on meso-and metathoracic femora; otherwise femora with dorsoapical processes undeveloped. *Color patterning*. Coxae concolorous with pleuron. Trochanters concolorous with femora. Femora color variable. Tibiae color variable, sometimes with upper fascia pigmented. Tarsi and claws reddish brown. *Chaetotaxy*. Coxae with a somewhat thick coat of long wispy setae. Trochanters with medium length wispy setae. Leg surface setae highly variable, as described in species descriptions. Tarsi ventrally with parasagittal rows of short, stiff, black setae bunched into twos, threes or fours, other surfaces with setae dense and somewhat appressed, short, slender, stiff, usually dark brown or black, but sometimes paler.

Wings (A2 Figs. 17–28). *Dimensions and shape*. FW and HW approximately coequal in length, HW sometimes slightly longer; HW tip extending beyond that of FW in specimens with wings folded back at rest; shape similar, FW broader than HW; wing apices smoothly curved anteriorly, usually somewhat broad but narrower than wing at midpoint, posteriorly often distinctly angulate but sometimes only very weakly acute, often pointed but sometimes smoothly curved; wings strongly narrowed at base, more so in HW, in FW anal process well-developed, narrow, elongate and apically acuminate, terminal cell extending to near apex of process or ending well before it, veins forming lateral margins of process separate or fused, in both wings margin smoothly reversing from concave to convex in basal one-fifth to one-third, wing broadest at or near wing midpoint, distally with posterior margin remaining convex to wing tip or becoming concave again (falcate), concavity usually more strongly expressed in females. *Venation*. FW. Costa and subcosta subparallel, diverging very slightly along length to pterostigma. Subcostal veinlets usually regularly spaced, in most species simple, but in a few highly irregular, bunching, converging, diverging, or forking, occasionally with secondary crossveins. Pterostigma represented by two to seven somewhat closely aggregated unforked and forked veinlets and an opaqueness in cell membranes adjacent to Sc-R anastomosis, these cells flanked by costal and apical area cells with brownish pigment; specifically, one to two cells proximad and at least proximal portions of several cells distad of anastomosis opaque to cream colored, and brown pigment absent along Sc+R distad of pterostigma, often giving distal margin of pterostigma a somewhat crescent shape with a longer arm along Sc+R. Sc+R striking posterior wing margin at to distinctly proximad of apical angle. Apical area broadest either anteromesally or mesally, narrowing distally, containing one to four long forked branches/veinlets divided by four to fifteen somewhat irregular crossveins. Subcostal area without crossveins. Presectoral area with five to ten primary crossveins, but these highly irregular and difficult to interpret, forking and connecting with numerous short crossveins and forming many irregular cells. Blyzocyte sets highly variable in number of cells in each set, in presence or absence of intercalary cells, and in expression of pigment. Rs forking from R one-fourth to one-third distance from wing base, with three to four well-defined forks loosely paralleling R; first fork (Rs_1) with a well-defined distal fork with several branches, Rs_4 and often Rs_5, if present, also with several branches; radial+postsectoral areas occupying one-third of distal part of wing, sometimes slightly more. Basal chiasma well-developed, cu-mp/1r-m moderately robust. Mp_2 forking from Mp near to Rs origin, joining Mp_2+Cua_1 before or after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin, but becoming somewhat irregular and zigzagged and sometimes difficult to distinguish from crossveins in distal section of vein. Cua forking proximal to Rs origin; cubital area occupying one-fourth to two-fifths of posterior half of wing. Cubital triangle long and narrow, prefork domain with seven to fifteen, sometimes bunched/forked/irregular crossveins, distal domain with zero to four crossveins; marginal cell present or absent, sometimes broadly joined to triangle, sometimes triangular and subdivided by crossveins, frequently allied with one or two paramarginal cells, but these often poorly developed or absent and marginal cell only connected by Cua_2+Cup. Anal area reduced to a single very narrow row of cells which broadens distally. 1A forked two-fifths to one-half distance from wing base to Cua fork, anterior branch fused with Cup, posterior branch runs to posterior wing margin. 2A short, briefly fused with 1A and fused distally with 3A in anterior portion of anal process. 3A short, forked at base of anal process, 3A anterior branch runs past anal process and forks again near posterior wing margin, its anterior branch variable in length and fused with 1A, its posterior branch runs to posterior wing margin; 3A posterior branch runs to anal process within which it forks again, usually connected by an oblique crossvein to 3A anterior branch. HW. Similar to FW except as follows. Apical area with four to sixteen somewhat irregular crossveins. Base of Mp robust. Mp_2 forked distad of Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, terminal portion sometimes difficult to distinguish from crossveins but apparently not fused with Mp_1; posterior medial area occupying one-fourth to one-third of posterior half of wing. Medial triangle long, often narrow, apex variable and usually somewhat short, broad and truncate or irregularly-shaped; prefork domain with five to 22 very short regular crossveins; distal domain very short, with zero to two crossveins. Anal area with one to several cells near wing base, obliterate mesally, then reappearing as a single narrow row of cells (which broaden distally) posterad of distal half of medial triangle. Crossvein cu-mp aligned with Cup, both roughly perpendicular to Cua, Cup striking a short and usually at least somewhat weakly developed 1A, presumably fused with it, Cup+1A running parallel to and touching posterior wing margin, sometimes fused with it in narrowest portion of wing. 2A and 3A very short and restricted to extreme wing base, 2A usually more weakly expressed, 2A and 3A curving toward one another and then fusing, forming a distinct almond- or ovoid cell, 2A continuing no further but anterior branch usually at least faintly visible, joining 1A near its anastomosis with Cup, 3A distally curved posterad to strike posterior wing margin. *Setae*. Costa of anterior margin bearing long slender setae at extreme base, then many short stiff curved black setae arranged in regular or irregular rows, reducing to a dense dorsal and ventral fringe of slightly longer setae near wing apex and continuing along posterior wing margin, this becoming less dense toward wing base until almost asetose in anal area, anal process of FW often glabrous but sometimes with some long wispy setae, posterior axillary setae long and slender. Veins, veinlets and crossveins of dorsal and ventral surfaces with short stiff curved black setae, but distribution differing among the species. Dorsal and ventral membranes often bearing slender curved dark brown setae, distribution also varying among the species. *Color and patterning*. Veins. Veins, veinlets and crossveins variable, pale yellowish to dark reddish brown. Membranes. Subcostal veinlets margined, sometimes diffusely and sometimes more distinctly, pigment often becoming denser in cells closest to pterostigma and nearly filling them; subcostal area completely pigmented except for gaps along Sc corresponding to pigmentless mesal portions of costal area cells; apical area blotch with pigment distribution variable and somewhat diagnostic; pigment distribution across wing variable, as given in species descriptions.

Abdomen (A2 Figs. 29–36). Approximately co-equal in length in males and females, generally broader in middle segments of females; segments without processes or setal tufts. *Tergum*. T1 short, sagitally separated by flexible membrane into subrectangular (in dorsal view) lateral plates, collectively slightly broader along anterior margin and bordered by a very narrow transverse groove and flange or carina, posterior margin collectively slightly broader than width of T2 acrotergite. T2 acrotergite length coequal to length of T1 plates, but often appearing shorter when abdomen is flexed up and acrotergite slides under T1, laterally and posteriorly sclerotized, mesally membranous, this contiguous with T1 membrane. T2 length (at midline) approximately coequal to width; T3 length approximately three times that of T2, T3 lateral margin usually straight but sometimes concave; T4 slightly shorter than T3, broadening posteriorly; T5–T8 each slightly shorter than the previous segment; T9 very short. *Color and patterning*. T1 plates variably colored, from partially pale to completely dark brown, membrane and sometimes plate mesal margins often much paler, and forming a broad sagittal stripe. T2 acrotergite typically darker in color, membrane often pale and appearing as a continuation of T1 stripe. Pattern on remaining tergites variable but repetitive, most developed in more derived species and best displayed on T3; tergite base color variable, dull yellow, reddish brown, or dark gray, usually paler anterolaterally near pleural membrane, dorsally on T2 and T3 where it forms a continuation of dorsal stripe, often at least posterodorsally on T4, sometimes on subsequent segments; posterolateral areas bearing a variably-expressed large dark brown or black macula, this subtriangular or bell-shaped with acute portion directed anterad, sometimes diffuse, the posterior portions of macula darkening and often distinctly crescent-shaped, posterior points of crescent sitting tangent or proximal to tergite posterior margin, posterior margin of crescent often thinly margined with pale pigment, this sometimes contiguous with pale posterior margin of tergite; tergite anterior margins often bearing a small sublateral diffuse dark macula. Posterolateral macula repeated on T2 through T8 in most species, usually short and diffuse and expressed only as a dark crescent on T2, on T4 large, broader anteriorly and diffuse, and more quadrate, diffuse and irregular on T5 through T8. Dark spots visible at bases of setae in paler areas of most tergites in most species. *Chaetotaxy*. Entire tergum bearing a sparse coat of long wispy dark setae, these densest laterally, longest on T1 and gradually shortening and becoming slightly stiffer on distal tergites. *Sternum.* S1 thin, carinate, in cross section quadrate with rounded corners. S2 acrotergite an inverted v-shape, short, apex touching T1 carina, sclerotized arms variable in thickness but generally narrow, area anterolaterad and posteromesad of arms membranous. S2 length coequal to width, with a membranous anterosagittal depression, somewhat swollen laterad of depression, posterior margin truncate. S3 length approximately three times that of S2, anteriorly narrower that S2, anterior margin acute, narrowly membranous laterad of apex, posterior margin straight, more-or-less evenly joined to S4. Subsequent sternites more-or-less evenly joined at margins. *Color and patterning*. S3 to terminal sternite more-or-less evenly brown, S3 and sometimes subsequent sternites with a large, diffuse posterolateral maculation. Dark spots often visible at bases setae. *Chaetotaxy*. S1 and S2 acrotergite glabrous, S3 to S9 in males, S3 to S7 in females with long wispy dark setae, these densest laterally, longest on T2 and gradually shortening and becoming slightly stiffer on distal sternites. *Pleural membrane.* Densely covered with microtrichia, dark grayish brown, sometimes with irregular diffuse yellowish or reddish brown mottling, often with dark spots bases of setae, setae moderately sparse, short, dark.

Male terminalia (A2 Fig. 31, 33). *Unmacerated specimens.* Ectoprocts slightly produced dorsally, often bulbous. S9 short, posterior margin weakly angled along sagittal line to form a keel; external color variable, from dull yellow to dark brown; external surface with numerous medium long, slender, stiff dark brown setae; interior surface with a broad dorsal sagittal carina, gonopore sometimes visible at innermost point of S9. Pulvini simple, short, sometimes extending slightly beyond S9 margin. Setae on ectoprocts and pulvini long, stiff. GPC often visible between pulvini, shiny. *Macerated specimens.* GPC, lateral view: length equal or slightly longer than height, apex rounded to acute, gonarcus dorsal outline weakly to strongly arched, dorsal margin subapically notched or not, pigment often fading to absent near apex, parameres usually only moderately sclerotized, darkest ventrally at grooves; ventral view: GPC often narrowed at base, width at broadest point narrower or broader than length, lateral margins smoothly curving and converging toward apex, wrinkled portion of each paramere about one-third to one-half overall paramere width, wrinkles numerous, parallel, oblique, inclined mesoapicad; shape of groove separating parameres (inter-parameral groove) a long very narrow spindle, slightly broader in apical portion, pelta also spindle-shaped, conspicuous or not, surface with numerous tiny pores (setal bases?).

Female terminalia (A2 Figs. 32, 34–36). *Unmacerated specimens.* Ectoprocts slightly produced dorsally, often bulbous. Ventrovalvae widely splayed distally. *Macerated specimens.* Distivalvae somewhat variable in size, height less than half that of ectoprocts, round to oblong. Ventrovalvae elongate, narrow, apices often slightly produced distad and sometimes ventrad, bulbous. Setae on ectoprocts, distivalvae, and ventrovalve approximately coequal in length. Linguella transverse, membranous, weakly bilobed, bearing short stiff setae. Interdental space shape variable, usually triangular to shield-shaped, glabrous. Interdens base weakly to strongly sclerotized, shape variable, interdens a short narrow blade oriented along sagittal line, blade profile shape variable.

Variation. In some specimens, colors overall darker, and patterns obscured by age, oily coatings, and possibly phenotypic variance.

Distribution.—Sub-Saharan Africa, southwestern Arabian peninsula.

Discussion.—McLachlan (1871) erected this genus without having personally examined a single specimen, but relied solely upon Hagen's (1853) description and (1862) figure of *lacerata*. Nevertheless, his observation that the genus was "sharply defined" and "without a parallel among the Holophthalmi" was astute at the time and is still borne out today.

Included species.—*alberti* Navás; *imperatrix* van der Weele; *lacerata* (Hagen); *larseni* Hölzel; *majesta* n. sp.; *rothschildi* van der Weele; *royi* Tjeder; *scopsi* Navás; *simplex* n. sp.; *waelbroecki* van der Weele.

Key to the species of* Tmesibasis*, adult males

1. Apex of antennae paler than remainder of flagellum (A2 Fig. 6), rarely completely brown; FW subcostal veinlets nearly equally spaced (A2 Fig. 99), generally simple, without crossveins (but sometimes one or two forked or more closely spaced than others) 2

1’. Apex of antennae completely brown (A2 Figs. 4, 5); FW subcostal veinlets conspicuously irregular (A2 Fig. 98) in both distribution and form (generally three or more irregular in at least one wing, forked, convergent and/or divergent, and/or connected by crossveins) 7

2(1). Wing membranes tinted brown (e.g., A2 Figs. 37, 51); FW length:width<3.65; C yellow on both sides of FW anal process; posterior marginal blotches prominent or reduced 4

2’. Wing membranes not tinted brown (e.g., Figs. 44, 46); FW length:width>3.75; C on proximal side of FW anal process dark brown, on distal side yellow; posterior marginal blotches always very reduced (A2 Fig. 46) 3

3(2’). Pronotum anterior lobes and posterior flange evenly brown, not mesally darkened (A2 Fig. 8); FW mesal blotch peaked but without a conspicuously broad mesal projection (A2 Fig. 46); FW mesal and subapical blotches close to one another or contiguous (A2 Fig. 46) [Kenya] .... ***imperatrix* van der Weele**

3’. Pronotum anterior lobes and posterior flange mesally darkened (A2 Fig. 9); FW mesal blotch with a conspicuously broad mesal projection (A2 Fig. 68); FW mesal and subapical blotches widely separated (A2 Fig. 68) [Kenya, Tanzania] .... ***majesta* n. sp.**

4(2). T1 plates usually paler laterally (dark spots visible at setal bases); T1 sagittal membrane not puckering anteriorly to form carinae in dried specimens 5

4'. T1 plates almost completely dark brown (dark spots thus not visible at setal bases); T1 sagittal membrane puckering anteriorly to form carinae in dried specimens (A2 Fig. 83, arrow) [Burkina Faso, Gambia, Nigeria, Senegal] .... ***royi*** **Tjeder**

5(4). HW mesal blotch at least thinly connected to subapical blotch, with height < one-third of width (A2 Fig. 88); FW mesal blotch height < one-half width (A2 Fig. 89), OR, blyzocyte 1 (and often 2) completely filled in with pigment (A2 Fig. 39) 6

5'. HW mesal blotch not connected to subapical blotch, with height at least one-half of width (A2 Fig. 51); FW mesal blotch height > one-half width (A2 Fig. 54); blyzocyte 1 rarely (and blyzocyte 2 never) completely filled in with pigment (A2 Fig. 51) [Malawi, Mozambique, Namibia, South Africa, Zambia, Zimbabwe] .... ***lacerata*** **(Hagen)**

6(5). Gap along margin of wings between subapical blotch and apical blotch devoid of pigment (A2 Fig. 37); HW mesal blotch with height ca. one-third width (A2 Fig. 37); blyzocyte 2 often completely filled in with pigment (A2 Fig. 39) [southeastern Democratic Republic of the Congo] .... ***alberti*** **Navás**

6'. Gap along margin of wings between subapical blotch and apical blotch connected by at least a thin line of pigment (A2 Figs. 88, 89); blyzocyte 2 not completely filled in with pigment (A2 Fig. 89); HW mesal blotches with height ca. one-fourth width (A2 Fig. 88) [Malawi, Tanzania, Democratic Republic of the Congo] .... ***scopsi* Navás**

7(1'). Apical area of wing with pigment along posterior margin (A2 Fig. 68); FW anal process with terminal cell ending well before apex (A2 Fig. 28); apical process of meso- and metathoracic femora long, acuminate (A2 Fig. 13); pigmented cell membranes without mesal granularity (e.g., A2 Fig. 99) 8

7' Apical area of wing without pigment along posterior margin, except sometimes as a very thin line (A2 Fig. 61); FW anal process with terminal cell extending to near apex (A2 Fig. 27); apical process of meso- and metathoracic femora short, not acuminate (A2 Fig. 12); pigmented cell membranes mesally with granularity, this often coarse and dark reddish brown (A2 Fig. 62) 9

8(7). Wings broad and strongly falcate, with apical angle acuminate (A2 Fig. 96); FW cubital area with nine or more well-developed cell rows meeting wing margin (A2 Fig. 96); mesal and subapical blotches broadly joined (A2 Fig. 98) [Côte d'Ivoire, Ghana, Togo, Democratic Republic of the Congo] ...... ***waelbroecki* van der Weele**

8'. Wings moderately broad and weaky falcate, with apical angle not acuminate (A2 Fig. 92); FW cubital area with eight or fewer well-developed cell rows meeting the wing margin (A2 Fig. 93); mesal and subapical blotches narrowly joined (A2 Fig. 93) [southern South Sudan, western Ethiopia] .... ***simplex* n. sp.**

9(7’). Mesal and subapical blotches well-developed, mesal and subapical blotches contiguous, or at least connected by a thin line of pigment (A2 Fig. 73, 75, 76) [Ethiopia, Kenya, Somalia] .... ***rothschildi*** **van der Weele**

9’ Mesal and subapical blotches small, not contiguous or connected by a line of pigment (A2 Figs. 59, 60) [Saudi Arabia, Yemen, Oman] .... ***larseni*** **Hölzel**

Key to the species of Tmesibasis, *adult females*

(not included: *scopsi*, *simplex*)

1. Apex of antennae paler than remainder of flagellum (A2 Fig. 6), rarely completely brown; FW subcostal veinlets nearly equally spaced (A2 Fig. 99), generally simple, without crossveins (but sometimes one or two forked or more closely spaced than others) 2

1’. Apex of antennae completely brown (A2 Figs. 4, 5); FW subcostal veinlets conspicuously irregular (A2 Fig. 98) in both distribution and form (generally three or more irregular in at least one wing, forked, convergent and/or divergent, and/or connected by crossveins) 6

2(1). HW subapical blotch strongly narrowed before joining apical blotch (e.g., A2 Fig. 52) 3

2’. HW subapical blotch only slightly narrowed, or expanding to join apical blotch (e.g., A2 Fig. 66) 4

3(2). HW mesal blotch with height ≥ width at base, mesal margin curved proximad (A2 Fig. 52); FW length:width < 3.7 [Malawi, Mozambique, Namibia, South Africa, Zambia, Zimbabwe] .... ***lacerata* (Hagen)**

3’. HW mesal blotch with height < width at base, mesal margin only weakly curved proximad (A2 Fig. 38); FW length:width > 3.75 [southeastern Democratic Republic of the Congo] .... ***alberti* Navás**

4(2’). Pronotum anterior lobes and posterior flange evenly brown, not mesally darkened (A2 Fig. 8); HW mesal and subapical blotches close to one another or contiguous, even only as a thin line of pigment (A2 Figs. 45, 82); HW subapical blotch only slightly narrowed, or expanding very slightly to join apical blotch at posterior reach of pterostigma (A2 Fig. 45) 5

4’. Pronotum anterior lobes and posterior flange mesally darkened (A2 Fig. 9); HW mesal and subapical blotches widely separated (A2 Fig. 66); HW subapical blotch expanding to join apical blotch at middle of pterostigma (A2 Fig. 66) [Kenya, Tanzania] .... ***majesta* n. sp.**

5(4). T1 plates almost completely dark brown (dark spots thus not visible at setal bases); T1 sagittal membrane puckering anteriorly to form carinae in dried specimens (A2

Fig. 83, arrow); HW mesal blotch wider at base than tall, not strongly peaked, mesal margin weakly curved proximad (A2 Fig. 82) [Burkina Faso, Gambia, Nigeria, Senegal] .... ***royi*** **Tjeder**

5’. T1 plates usually paler laterally (dark spots visible at setal bases); T1 sagittal membrane not puckering anteriorly to form carinae in dried specimens; HW mesal blotch narrower at base than tall, strongly peaked, mesal margin strongly curved proximad (A2 Fig. 45) [Kenya] .... ***imperatrix*** **van der Weele**

6(1’). Apical area of wing with pigment along posterior margin (e.g., A2 Fig. 68); FW anal process with terminal cell ending well before apex (A2 Fig. 28); apical process of meso- and metathoracic femora long, acuminate (A2 Fig. 13, *fdp*); pigmented cell membranes without mesal granularity (e.g., A2 Fig. 99) [Côte d’Ivoire, Ghana, Togo, Democratic Republic of the Congo] .... ***waelbroecki*** **van der Weele**

6’ Apical area of wing without pigment along posterior margin, except sometimes as a very thin line (A2 Fig. 61); FW anal process with terminal cell extending to near apex (A2 Fig. 27); apical process of meso- and metathoracic femora short, not acuminate (A2 Fig. 12, *fdp*); pigmented cell membranes mesally with granularity, this often coarse and dark reddish brown (A2 Fig. 62) 7

7(6’). Mesal and subapical blotches well-developed, mesal and subapical blotches contiguous (at least connected by a thin line of pigment) or nearly so (A2 Fig. 74) [Ethiopia, Kenya, Somalia] .... ***rothschildi* van der Weele**

7’ Mesal and subapical blotches small, not contiguous or connected by a line of pigment, well-separated [Saudi Arabia, Yemen, Oman] .... ***larseni* Hölzel**

Tmesibasis alberti *Navás*

(A2 Figs. 3, 26, 31, 33, 36–43, 104)

Tmesibasis alberti Navás, 1912

—Navás 1912 r#561: 91, pl. III fig. 2 {OD, DIS, ET, TL}

[*Tmesibasis imperatrix* van der Weele, 1909]

—Esben-Petersen 1936 r#180: 199 {GD, SR}

Etymology and nomenclatural notes.—*alberti;* a Latinized noun in the genitive case, named by Navás 1912 for S. M. Albert I, the king of Belgium at the time of writing (see ‘Discussion’, below).

Diagnosis.—Wing venation dense. Blotch pigment reddish-brown. Male: blyzocytes 0–2 filled in completely or nearly so with pigment, blyzocyte sets 3–5 reduced in size; HW mesal blotch height ca. one-third to one-half width; gap along HW margin between subapical and apical blotch completely devoid of pigment; proximal one half to two-thirds of hyaline area with brownish tint. Female: FW length:width > 3.75; wings weakly falcate; apical areas narrow, unproduced anterolaterally; apical angle acute; mesal blotch proximal margins nearly straight, not strongly curving toward wing base; mesal and subapical blotches proximate or narrowly contiguous; subapical blotches constricted before joining apical blotches.

Distribution (A2 Fig. 104).—Southeastern Democratic Republic of the Congo.

Autapomorphies.—Pronotum anterior flange lobes medially dark brown to black (char. 7, state 1); blyzocytes 0, 1 and 2 of males completely or nearly completely pigmented (char. 21, state 1); FW subapical blotch in males separated from apical blotch in radial area (not apical area) by a complete gap in pigment (char. 24, state 3); in males, FW apical blotch mesal cells with pigment voids unaligned (char. 26, state 3).

Description.—

Size (mm). Male: length of body 24-(27)-30, abdomen 16-(19)-22, forewing 26-(30)-32, hind wing 26-(30)-32, antennae 34-(37)-40. Female: length of body 30, abdomen 21, forewing 36, hind wing 37, antennae 38.

Head (A2 Fig. 3). Occiput brown. Postorbital sclerite even in width, broadening slightly behind depression of eye, pale brown. Vertex brown. Anterior extra-torular sclerites orangish brown, often pale yellow along distal margin. Frons brown or orangish, setae golden brown. Clypeus orangish brown, slightly paler mesally, setae commencing mesally, golden brown. Labrum orangish brown, setae brown. Paraocular band dark to orangish or yellowish brown, usually glabrous, but occasionally with a few small dark slender brown setae. Anterior orbital sclerite sometimes concolorous with paraocular band, but often orange or yellow. Posterior genal triangle concolorous with paraocular band. Mandibles pale translucent brown. Maxillary stipes and palpomeres pale orangish brown, stipes and palpomere 1 setae brown and golden brown, palpomere apical whorl setae pale brown. Submentum, mentum and palpigers very pale orangish brown, setae golden brown; labial palpi orangish brown, setae golden brown; ligula pale orangish. Eyes posteriorly very weakly bilobed. *Antennae.* Scape orangish to brown, setae pale yellow with some dark brown setae mixed in laterally. Pedicel distal margin orange or yellow; pore moderately large. Flagellum with 43 flagellomeres, including club, whose beginning is indistinguishable, color yellowish in basal half, becoming brown in distal half, surface of basal flagellomeres facing eye slightly darkened, apical five to six flagellomeres of club yellow; verticil fringes on basal five to six flagellomeres; males with setitori somewhat to well-developed in distal half of flagellum. Club poorly distinguished, apical two or three flagellomeres coequal to their width.

Thorax. *Cervix*. Dorsal cervical plates round, brown, setae golden brown. Cervical sclerite dull yellowish brown, anterior setae yellow. Ventral cervical plate yellow to orangish. *Pronotum*. Length approximately two-fifths that of mesonotum. Pronotum anterior flange lobes brown, anteromesal surfaces darkened, in some specimens as dark as velvety spots, setae brown. Medial transverse band mesally brown, sublaterally pale brown, lateral setae brown; posterolateral knob dorsally yellow, laterally dark brown. Posterior flange sagitally pale brown, parasagittally brown and often considerably darkened, sublaterally brown; setae brown. *Mesonotum*. Prescutum subauriculate, sagittal sulcus weak; lobe setae brown. Scutum with velvety spot large, oblong , its long axis directed anterad and slightly oblique toward lateral margins of mesoprescutum and pronotum, often an elongate obscure slightly dark brown stripe positioned laterad of velvety spot and directed toward mesolateral margin of lobe; setae golden brown. Scutellum posterior swelling bearing a transverse yellow stripe, surface posterad of stripe often dark brown; setae brown. Subscutellum mesally yellow, otherwise brown. Postnotum brown. *Metanotum*. Paraprescutum dark brown. Prescutum mesally yellow, laterally dark brown. Scutum brown, velvety spot texture well-developed, setae brown. Scutellum sagittal surface with a broad, very diffuse longitudinal pale brown or dull yellowish stripe, posterior swelling with a transverse yellow stripe, lateral setae brown. *Pleuron*. Mesanepimeron projection short; dorsal margin of meso- and metabasisternum a narrow yellow transverse stripe, ventral surface dark brown, mesothoracic subalar membrane posterior area yellow; setae golden brown.

Legs. *Morphology*. Femora with dorsoapical processes well-developed. *Color patterning*. Coxae more-or-less evenly brown. Trochanters and femora reddish brown to somewhat dark brown, apical process yellow dorsally along margin and on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color circumscribing tibia at extreme base, but quickly narrowing into a longitudinal posterodorsal stripe that continues to narrow distally. *Chaetotaxy.* Coxae setae golden yellow or golden brown. Trochanter setae brown. Femur setae dense, long, slender, brown or golden brown. Tibia setae somewhat dense, medium long, slender, mixed yellow, golden brown and brown.

Wings (A2 Figs. 26, 37–39). *Dimensions and shape.* Long, FW length coequal to or often very slightly less than that of HW, but apex of HW extending well beyond that of FW in unspread specimens; anterior margins straight or very slightly convex; wing apical angles acute and pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal half, in HW of males and both wings of female posterior margin past midpoint somewhat to highly falcate. Wings in females relatively larger and more slender than those of males with similar body size. *Venation*. Slightly denser and with more cells than in other species, except for perhaps *lacerata* and *scopsi*. FW. Subcostal veinlets slightly irregularly spaced, essentially perpendicular to subcosta and parallel to one another, zero to four (usually one to three instances of bunching, convergence or divergence, or forking. Pterostigma with four to six veinlets; pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking wing margin at inflection point of anterior and posterior margins. Apical area broadest mesally, containing one to three long forked branches/veinlets connected by five to thirteen somewhat irregular crossveins. Presectoral area with approximately five to eight primary crossveins. Males with bc0 cell(s) entire from R to Mp but completely filled with pigment, bc1, bc2, and bc3c supertending Mp, Rs, and Rs_2 respectively but separated from R by several small irregular cells, usually completely filled with pigment but occasionally only anteriorly margined, bc4c supertending Rs_3 but separated from R by several small irregular cells, anteriorly margined with pigment, bc5c supertending Rs_4, bc5a entire to R, sometimes separated from bc5b/c, bc5b/c separated from R by several small irregular cells, dorsally margined with pigment; females with bc0 cell(s) entire from Mp to R and margined posteriorly with pigment, remaining blyzocytes entire from subtending vein to R, and only very thinly and weakly margined, mostly devoid of pigment, bc5 set with four (left wing) or five (right wing) cells. Rs forked from R approximately one-fourth distance from wing base, with three and sometimes four well-defined anterior forks loosely paralleling R; Rs_5 also with several branches; radial+postsectoral areas roughly occupying distal third of wing. Crossvein cu-mp/1r-m robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 usually well after Cua fork but occasionally slightly before (JRJ_01002); Mp_2+Cua_1 paralleling Mp_1 to wing margin, but becoming somewhat irregular and crooked and sometimes difficult to distinguish from crossveins distad of inflection point. Cua forked proximal to Rs origin; cubital area roughly occupying mesal third of posterior half of wing. Cubital triangle prefork domain with eight to fourteen crossveins, distal domain with one to three sometimes forked or irregular crossveins; marginal cell often present, sometimes subdivided by crossveins, frequently allied with one or two paramarginal cells, but these sometimes poorly developed and only Cua_2+Cup prominent. Anal area cells broadening somewhat distally. 1A appearing to strike and robustly fuse with posterior wing margin approximately halfway from wing base to Cua fork, a very weakly-developed small portion forked anteriorly to fuse with Cup. HW. Similar to FW except as follows. Sc+R striking wing margin just proximad of inflection point of anterior and posterior margins along posterior margin. Apical area with five to fourteen somewhat irregular crossveins. In males, bc0 to bc5 supertending Mp_1, Mp_1, Rs, Rs_2, Rs_3, and Rs_4/Rs_5 respectively, but separated from R by several small irregular cells, bc1 usually filled with pigment but occasionally pale mesally, bc2 to bc5 small, usually thickly margined and mesally pale; in female bc5 set with four cells. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, well-defined and not fused with Mp_1; posterior medial area occupying mesal third of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with five to fifteen very short regular crossveins, mesal ones often obliterated by narrowness of row; distal domain lacking crossveins; marginal cell and one or more paramarginal cells present. Anal area with a single triangular cell near wing base. Cup striking a short and weakly developed 1A, Cup+1A fused with Cua at base of narrowest portion of wing, Cup+1A+Cua subsequently fused with posterior wing margin at narrowest portion of wing, separating from margin as wing begins to widen again. 2A more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch visible. *Setae*. Costa basal setae brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: ventral membranes in costal area, and dorsal and ventral membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, blyzocytes of radial area, and unpigmented distal portion of radial area near apical area. *Color and patterning*. Veins. Costa yellow, Sc pale reddish, FW Mp and HW Mp_2 reddish brown, most remaining veins, veinlets and crossveins pale yellowish or reddish. Membranes. Subcostal veinlets thickly and diffusely margined with reddish brown pigment; apical area blotch with pigment variable, absent near pterostigma and in a narrow mesodistal stripe near wing margin, also a few mesal cells bordering radial area only margined; pigment more-or-less completely filling cells in anterior blotch, distal cells of radial area along Sc+R, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), cubital area (HW: posterior medial area) near fork, and basal and distal portions of anal area, including anal process; proximo-mesal cells of anal area thinly margined, disto-mesal cells more thickly margined. Male: Basal two-thirds of hyaline portions of both wings smoky reddish brown, tint becoming fainter distally. FW mesal blotch triangular but variable in shape, shorter than wide, usually only thinly touching subapical blotch if at all; FW subapical blotch flatly triangular, one-half to two thirds as tall as mesal blotch, much shorter than wide, separated from apical blotch by a pigmentless gap one-third to one-half mesal subapical width; HW mesal blotch shorter than in FW but not usually considerably flattened, height ca. one-third width, often at least thinly joined to subapical blotch; HW subapical blotch flatly triangular, about half as tall as mesal blotch, much shorter than wide, separated from apical blotch by a pigmentless gap one-third to one-half subapical blotch width. Female: Hyaline membranes lacking any color. FW mesal blotch curved triangular, height about half width, narrowly separated from subapical blotch; FW subapical blotch flatly triangular, half as tall as mesal blotch, much shorter than wide, joining apical blotch but narrowing as it does so; HW mesal blotch similar in size and shape to that in FW, very thinly separated from subapical blotch; HW subapical blotch similar in size and shape to that in FW, narrowing before thinly joining apical blotch. All blotches and membranes of male and female with a certain subtle reddish-orange hue, very slightly different from that of other species.

Abdomen (A2 Fig. 31, 33). *Tergum.* T1 sagittal depression membrane somewhat loose, but only rarely drawn into longitudinal wrinkles or carinae along margins of groove and puckering anteriorly; plates often mostly dark brown, but lateral area frequently paler with dark spots at bases of setae, sagittal depression and mesal margins of plates yellow, forming a broad stripe one-fourth width of segment. T2 acrotergite sagittal membrane yellow or dull brown to dark brown, appearing as a continuation of T1 stripe; T2 posterolateral macula short, crescent-shaped, posterior margin of macula and tergite margined with pale yellow or gray. T3 base color reddish or yellowish brown; posterolateral macula approximately half length of tergite or longer, diffuse, sometimes irregular, elongate, narrowly triangular, posterior margin of macula and tergite margined with pale yellow or gray; dark brown spots usually present at bases of setae. T4 anterolateral and posterosagittal surfaces pale reddish or yellowish brown, anterior margin with small sublateral black diffuse maculae immediately posterad of T3 crescents, posterolateral area with a diffuse dark brown macula similar in shape to that on T3 but slightly more robust, posterior margin of macula and tergite margined with pale yellow or gray; dark brown spots usually present at bases of setae. T5 patterning similar to that of T4, but posterolateral maculae usually narrow longitudinally and very diffuse. T6–T8 base color grayish brown, posterolateral macula very diffuse and poorly expressed, surfaces bearing small diffuse dark brown spots at bases of setae. T9 reddish to dark brown. T1 to T3 surfaces, not including T2 acrotergite, with numerous long slender dark brown setae, these continuing but shortening gradually along T4, and then more-or-less consistently medium length to T9. *Sternum*. S1 dull reddish to pale brown. S2 acrotergite arms somewhat slender, gap between them round and somewhat small. S3 posterior maculae moderately large, sometimes diffuse, yellow, sometimes darkened to reddish or orangish brown. S4 and S5 sometimes with orangish or dark brown maculae posteriorly similar to S3. S5–S7 brown, a small diffuse dark brown spot at base of each seta. S2 acrotergite to S3 with numerous medium length slender dark brown setae, these continuing but moderately short from T3 to sternum apex.

Male terminalia (A2 Figs. 31, 33, 40, 41). *Unmacerated specimens*. Ectoprocts slightly produced and bulbous dorsally, reddish and yellowish brown mesally, dark brown along posterior margin. S9 reddish to dark brown, interior surface reddish to dark brown. Pulvini extruding beyond S9 margin, reddish to dark brown. GPC slightly visible between pulvini, glossy, color variable, reddish brown or yellowish and dark brown. *Macerated specimens*. Pulvini length two to three times width and half to two-thirds length of GPC. Setae long, stiff, dark, co-equal in length on ectoprocts and pulvini. GPC, lateral view: basally somewhat broad, dorsal and ventral margins subparallel, dorsal surface slightly darkened, pigment becoming fainter in apical third, dorsal margin often mesally slightly notched, parameres brown, apex slightly more acute; ventral view: base broad, width approximately coequal to overall length; lateral margin basally subparallel, first diverging slightly at base, then converging again at mid length toward apex, apical portion converging strongly, acute, apex rounded or not, grooved portion of each paramere one-third to one-half width of entire paramere, somewhat darkened, orangish; inter-parameral groove slightly broader in apical portion, pelta color very pale, inconspicuous.

Female terminalia (A2 Figs. 36, 42, 43). *Unmacerated specimen*. Ectoprocts dorsally somewhat produced, orangish brown. Ventrovalvae orangish brown. Linguella and distivalvae orangish brown. *Macerated specimen*. Distivalvae large, height approximately half that of ectoprocts, oblong, well separated from one another, very proximate to ectoprocts and linguella. Ventrovalvae only slightly elongate, slightly broad, apices somewhat bulblike ventrad but not protruding distad in lateral view. Linguella medium in size, membranous, somewhat well-developed in paired transversely arranged lobes, bearing short slender stiff brown setae. Interdental space shape a small wide triangle; interdens sclerotized base shape a somewhat large flat diamond, sclerotized dark, nearly filling interdental space, sagittal blade profile somewhat high, length short, evenly curved.

Variation. Interior surface of male S9 only visible in very few unmacerated specimens. Lectotype varying from other dissected specimens in the following traits:

GPC in lateral view lacking mesal notch and apically slightly more blunt, in ventral view slightly narrower overall, apex less acute and more rounded.

Primary type.—

Tmesibasis alberti Navás, 1912. Holotype ♂, RMCA, examined (A2 Figs. 37, 39). *Type locality*: Democratic Republic of the Congo, Kasenga [-10.622773°, 26.758409°], 1127 m. *Label data*: "TYPE /// MUSÉE DU CONGO Kasenga 2-11-1912 Dr. Bequaert /// R. DÉT. C 220 /// Tmesibasis Alberti Nav. /// Typus /// Lectotypus Tmesibasis alberti Navás ♂ design. Bo Tjeder 1977 Terminalia in glycerin in micro-vial /// 00710p /// HOLOTYPE Tmesibasis alberti ♂ det. J. R. Jones 2013 /// JRJ_01240". *Condition*: good, right antennae broken off at base but reattached with glue. *Notes*: In his original description, Navás did not explicitly designate a type specimen, nor indicate how many specimens were in the type series. The fact that he gave a single length (as opposed to a range of lengths) for each of the features he measured, and that he recorded information for a single collection locality, date, and collector, suggest that the type series consisted of a single specimen. The RMCA specimen above bears three previously applied 'type' labels, matches the descriptions and measurements given by Navás, and is taken here to be the holotype of *T. alberti* (Tjeder's lectotype label is ignored).

Additional material examined.—*Democratic Republic of the Congo*: Katanga [BMNH: 4 ♂♂, JRJ_01263, JRJ_01264 (A2 Figs., 40, 41), JRJ_01265, JRJ_01272; FSCA: 1 ♂,

JRJ_01002; MHNG; 1 ♂, JRJ_01003, 1 ♀, JRJ_01004 (A2 Figs. 38, 42, 43); RMCA: 1 ♂, JRJ_01243].

Natural history.—As recorded on specimen labels, several adult specimens were collected “at light”.

Discussion.—Males of *T. alberti*, *T. lacerata*, *T. scopsi* and *T. royi* are similar and can be difficult to distinguish from one another. However, several diagnostic features were discovered for each species that also correspond with fairly well-defined geographic distributions. In the case of *T. alberti*, these include blyzocytes 1–2 being completely filled with pigment, the shapes and positions of the posterior blotches of the wing, the higher density of cell rows and cells throughout the wing, and the particular reddish hue of the wing blotches and membranes.

The female of *T. alberti* is here described for the first time. It is larger and has different wing shape and blotch patterns than the male, and during early examinations it was not immediately evident that the male and female were conspecific. Several factors were discovered, however, which support this relationship. These include the dense wing venation, reddish hue of the wing blotches and membranes, large size, and, in the apical blotches, the mesal cells with pigment voids being margined and unaligned. The single female examined (JRJ_01004, which Esben-Petersen [1936] identified as *T. imperatrix*) and all males come from six highly clustered localities in southeastern Democratic Republic of the Congo (A2 Fig. 104).

Regarding King Albert, for whom Navás named this species, Navás (1912) wrote, "au cours du voyage qu'il fit dans la colonie du Congo belge, s'attacha à recueillir des spécimens de la faune entomologique des régions traversées, donnant ainsi une preuve de grand intérêt à la science qui nous est chère" ['during the journey he made in the Belgian Congo colony, he dedicated himself to collecting specimens of the insect fauna of the regions crossed, giving proof of his great interest in the science that is dear to us']. Perhaps Navás felt inclined to provide a name with royal significance, in following with van der Weele's (1909) use of the name *imperatrix* for a previous species, to which Navás compared *T. alberti* (see 'Discussion' for *T. imperatrix*, below).

Tmesibasis imperatrix *van der Weele*

(A2 Figs. 15, 17, 18, 20, 44–50, 104)

Tmesibasis imperatrix van der Weele, 1909

—van der Weele 1909.01.05 r#420: 91, fig. 56 {OD, DIS, TL, TR, TS}; Navás 1914 r#626: 4 {DIS, GD, MOR, TL, TR, TS}

Etymology and nomenclatural notes.—*imperatrix*: impero (Latin), 'commander-in-chief, general, ruler'; -trix (Latin) suffix signifying agent, usually feminine: thus, 'empress' (see 'Discussion', below).

Diagnosis.—Similar to *majesta* (males with slender wings lacking brownish tint in hyaline membrane, and blotches reduced; females with long, slender, highly falcate wings, HW subapical blotches expanded to meet apical blotch, these not or only very slightly narrowed distad of midpoint), but differing as follows. Labrum orangish brown; pronotal anterior flange lobes and posterior flange evenly brown. Male: FW mesal blotch base flatly triangular, mesal peak short and narrow; HW mesal and subapical blotches proximate to one another, subapical blotch equal or subequal to height of mesal blotch. Female: apical area expanded anterolaterally, HW apex margin nearly perpendicular to anterior margin; HW subapical blotch an even, somewhat narrow band separated from mesal blotch by a gap less than height of subapical blotch.

Distribution (A2 Fig. 104).—Kenya, Tanzania.

Autapomorphies.—FW apex in females with anterolateral margin expanded, apex of wing produced distinctly distad of apical angle (char. 11, state 1).

Description.—

Size (mm). Male: length of body 22-(25)-26, abdomen 16-(18)-19, forewing 29-(31)-32, hind wing 30-(31)-33, antennae 36-(37)-40. Female: length of body 20-(24)-27, abdomen 12-(16)-19, forewing 32-(34)-34, hind wing 33-(34)-35, antennae 36-(38)-40.

Head. Occiput yellowish brown. Postorbital sclerite approximately even in width, broadening very slightly behind depression of eye and again adjacent to dorsal cervical plate, pale brown. Vertex orangish brown, mesal surface of each lobe darker brown. Anterior extra-torular sclerites orangish brown, occasionally paler along distal margin. Frons brown or orangish, setae brown or golden brown. Clypeus orangish brown, slightly paler mesally, setae commencing mesally, golden brown. Labrum dull orangish brown, setae brown. Paraocular band dark to orangish or yellowish brown, glabrous. Anterior orbital sclerite sometimes concolorous with paraocular band, but often orange or yellow. Posterior genal triangle concolorous with paraocular band. Mandibles pale translucent yellowish or orangish brown. Maxillary stipes and palpomeres pale orangish brown, stipes and palpomere 1 setae brown and golden brown, palpomere apical whorl setae pale brown. Submentum, mentum and palpigers very pale orangish brown, setae golden brown; labial palpi orangish brown, darkening to brown in distal palpomeres, setae golden brown; ligula pale orangish, with some very short slender golden brown setae. Eyes posteriorly only very weakly bilobed. *Antennae.* Scape orangish to brown, setae pale yellow with some dark brown setae mixed in laterally. Pedicel distal margin orange or yellow; pore moderately large. Flagellum with 38-41 flagellomeres, including club, whose beginning is indistinguishable, basal flagellomeres difficult to distinguish;

flagellum color yellowish in basal half, becoming brown in distal half, surface of basal flagellomeres facing eye considerably darkened, apical three to six flagellomeres of club yellow; verticil fringes on basal five to six flagellomeres; in males setitori somewhat to well-developed in distal half of flagellum. Club poorly distinguished, apical two or three flagellomeres co- or subequal to their width.

Thorax. *Cervix*. Dorsal cervical plates round, brown, setae golden brown. Cervical sclerite pale yellow, anterior setae yellow. Ventral cervical plate small, yellow to orangish. *Pronotum*. Length approximately two-fifths that of mesonotum. Pronotum anterior flange lobes brown, sometimes slightly darkened anteromesally, setae brown. Medial transverse band anterolateral margin acute, sometimes drawn into a short peak, color brown, lateral setae brown; posterolateral knob dark brown distally. Posterior flange brown; setae brown. *Mesonotum*. Prescutum auriculate, sagittal sulcus weak; lobe setae brown. Scutum with velvety spot large, oblong , its long axis directed anterad and slightly oblique toward lateral margins of mesoprescutum and pronotum, lateral surface often with a small narrow transverse velvety spot-like darkening where it meets wing near base of radius; setae brown. Scutellum posterior swelling bearing a transverse yellow stripe, surface posterad of stripe often dark brown; setae brown. Subscutellum mesally yellow, otherwise brown. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum mesally yellow, laterally dark brown. Scutum brown, velvety spot texture well-developed, setae brown. Scutellum sagittal surface with a broad, very diffuse longitudinal pale yellow stripe, posterior swelling with a transverse yellow stripe, lateral setae brown. *Pleuron*. Mesanepimeron projection short; subalar membrane posterior area yellow; setae golden brown.

Legs (A2 Fig. 15). *Morphology*. Femora with dorsoapical processes well-developed.Tibial spurs and tarsal claws robust. *Color patterning*. Coxae yellowish or orangish to dark brown. Trochanters and femora reddish brown to somewhat dark brown, apical process yellow dorsally along margin and on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color circumscribing tibia at extreme base, but quickly narrowing into a longitudinal posterodorsal stripe that continues to narrow distally. *Chaetotaxy*. Coxae setae golden yellow or golden brown. Trochanter setae brown. Femur setae dense, long, slender, golden yellow, golden brown and brown. Tibia setae somewhat dense, medium long, slender, golden brown and brown.

Wings (A2 Figs. 17, 18, 20, 44–46). *Dimensions and shape*. Long, FW length coequal to or often very slightly less than that of HW, but apex of HW extending well beyond that of FW in unspread specimens; FW slightly broader than HW; anterior margins straight or very slightly convex; wing apical angles acute and pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal half, in both wings posterior margin past midpoint somewhat to highly falcate in most specimens, more so in HW and more so in females. Wings in females relatively larger than those of males with similar body size, wings of males much more slender. *Venation*. FW. Subcostal veinlets slightly irregularly spaced, essentially perpendicular to subcosta and parallel to one another in basal half, gradually becoming slightly inclined distad in distal half, zero to four (usually just one or two) instances of bunching, convergence or divergence, or forking. Pterostigma with four to six veinlets; pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking wing margin just proximad of inflection point of anterior and posterior margins along posterior margin. Apical area broadest mesally, containing one to three long forked branches/veinlets divided by five to thirteen somewhat irregular crossveins. Presectoral area with approximately five to ten primary crossveins. Males with bc0 cell(s) usually entire from R to Mp and completely filled with pigment, rarely mesally pale, bc1, bc2, bc3b, and bc4b supertending Mp, Rs, Rs_2, and Rs_3 respectively but separated from R by several small irregular cells, blyzocytes only anteriorly margined, bc5c supertending Rs_4, sometimes separated from R by several small irregular cells, dorsally margined with pigment; females with bc0 cell(s) usually entire from Mp to R and completely filled with pigment, bc1, bc2, bc3b, bc4b, bc5d sometimes entire from subtending vein to R, but often separated by several small irregular cells, anteriorly margined, mostly devoid of pigment. Rs forked from R approximately one-third distance from wing base, with three well-defined anterior forks loosely paralleling R; Rs_4 also with several branches; radial+postsectoral areas roughly occupying distal third of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 either slightly before or after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin, but becoming somewhat irregular and sometimes difficult to distinguish from crossveins distad of inflection point. Cua forked proximal to Rs origin; cubital area roughly occupying mesal third of posterior half of wing. Cubital triangle prefork domain with ten to fifteen crossveins, distal domain with one to four sometimes irregular crossveins; marginal cell present, frequently allied with a well-developed paramarginal cell. Anal area cells broadening somewhat distally. 1A forked approximately halfway from wing base to Cua fork, anterior branch fused with Cup, posterior branch fused with posterior wing margin. HW. Similar to FW except as follows. Apical area with four to fourteen somewhat irregular crossveins. In males, bc0 to bc5 supertending Mp_1, Mp_1, Rs, Rs_2, Rs_3, and Rs_4 respectively, not separated from R by small irregular cells; in female bc0 usually completely filled with pigment. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 almost to wing margin, terminal portions sometimes forked and difficult to distinguish from crossveins; posterior medial area occupying one-fourth of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with 13-22 very short regular crossveins, mesal crossveins not obliterated; distal domain lacking crossveins, sometimes indistinguishable; in males, marginal cell and usually one, but sometimes two, paramarginal cells present; in females, a single marginal cell present, this contiguous with distal domain, not separated by a crossvein. Anal area with a few cells near wing base. Cup striking 1A, Cup+1A fused with Cua before narrowest portion of wing base, Cup+1A+Cua subsequently fused with posterior wing margin at narrowest portion of wing, separating from margin as wing begins to widen again. 2A sometimes more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch visible. *Setae*. Costa basal setae brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: ventral membranes in costal area, and dorsal and ventral membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, blyzocytes of radial area, and unpigmented distal portion of radial area near apical area. *Color and patterning*. Veins. Costa and all major longitudinal 'down' veins yellow, all 'up' veins a dull yellowish brown, most remaining veins, veinlets and crossveins pale yellowish or dull yellowish brown. Membranes. Subcostal veinlets thinly margined with reddish brown pigment; apical area blotch with pigment variable, absent near pterostigma, in a short narrow mesodistal stripe near wing margin, and mesodistally along Sc+R, also a few mesal cells only margined; pigment more-or-less completely filling cells anterior blotch, basal half of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), sometimes cubital area (HW: posterior medial area) near fork, and basal and distal portions of anal area, including anal process; many cells only margined in mesal portions of mediocubital area (HW: anterior medial area) proximad of Rs origin and in mesal portions of cubital triangle (HW: medial triangle). Male: Hyaline portions of both wings devoid of smoky pigment. FW mesal blotch greatly reduced, very flatly triangular, sometimes mesally peaked but if so peak acuminate and not apically broadened, blotch width greater than three times height, usually not touching subapical blotch but if so only thinly; FW subapical blotch sometimes weakly and flatly triangular, usually a flat narrow band of pigment narrowing slightly before touching apical blotch; HW posterior marginal blotches Similar to FW but mesal blotch even more reduced. Female: Hyaline membranes lacking any color. FW mesal blotch large, curved triangular, height co- or very slightly sub-equal to width, separated, sometimes broadly, from subapical blotch; FW subapical blotch rising in a somewhat smooth slope from margin to apical area, anterodistal portion touching posterior reach of pterostigma, sometimes narrowing very slightly mesally; HW mesal blotch similar in size and shape to that in FW, separated from subapical blotch; HW subapical blotch similar in shape to that in FW, but more elongate and narrowing slightly before joining apical area.

Abdomen. Tergum. T1 plates dark brown, sagittal depression and mesal margins of plates yellow, forming a broad stripe. T2 acrotergite membrane yellow, appearing as a continuation of T1 stripe. T2 sagittally yellow to orangish or dull reddish brown, appearing as a dull continuation of T1 stripe, laterally brown, posterolateral macula crescent shaped, dark. T3 base color very pale reddish and/or yellowish brown, posterolateral macula approximately one-half to three-fifths length of tergite, elongate triangular, diffuse and somewhat irregular; setae with dark brown spots at their bases. T4 dorsal surface almost completely dark brown, anterolateral and posterosagittal surfaces pale reddish or yellowish brown, posterolateral macula similar to that of T3 but slightly more robust; setae each with a dark brown spot at its base. T5 patterning as in T4. T5–T8 base color orangish or reddish brown, posterolateral macula diffuse and irregular; each seta with a dark brown spot at its base. T9 brown, mesally paler. *Sternum.* S1 brown. S2 acrosternite arms narrow. S2 orangish to brown. S3 brown, posterior sublateral maculae less pronounced in females, in males moderately large, diffuse, orange to yellow, with dark brown anterior and posterior borders; dark brown spots at bases of setae. S4 sometimes with orange or dark brown sublateral maculae similar to S3; S4–S7 brown, a dark brown spot at base of each seta.

Male terminalia (A2 Figs. 47, 48). *Unmacerated specimens.* Ectoprocts only very slightly produced dorsally, dark brown. Other surfaces dark brown, or colored, as follows. S9 interior surface orangish yellow to reddish brown. Pulvini extruding very slightly beyond S9 margin, orangish yellow to reddish brown. Gonarcus visible between pulvini, large, dark reddish brown, mesally yellowish. *Macerated specimens.* Pulvini length approximately two-thirds that of gonarcus, two times width. Setae long, stiff, dark, co-equal in length on ectoprocts and pulvini. GPC, lateral view: length medium, basally broad, dorsal surface weakly arched, darkened, pigment absent in a small triangle at apex, parameres brown, apex slightly more blunt; ventral view: width at broadest point co- or slightly sub-equal to overall length, overall shape approximately round, base slightly narrowed, lateral margins diverging at immediate base, then evenly curved and converging toward apex, apex moderately acute, rounded, wrinkled portion of each paramere one-third to one-half width of entire paramere, slightly darkened, orangish to brown; inter-parameral groove slightly broader in apical portion, pelta yellowish, somewhat conspicuous.

Female terminalia (A2 Figs. 49, 50). *Unmacerated specimens.* Ectoprocts brown. Ventrovalvae brown, apical margins orangish to brown. Linguella and distivalvae brown to reddish brown. *Macerated specimens.* Distivalvae small, height approximately two-fifths that of ectoprocts, globose, well separated from one another, very proximate to ectoprocts. Ventrovalvae slightly elongate, moderately narrow, in lateral view apices somewhat bulblike. Linguella small, mostly membranous, dorsal portion appearing as weakly sclerotized paired transversely arranged lobes, bearing short stiff brown setae. Interdental space shape triangular; interdens sclerotized base shape sub-rectangular, only moderately sclerotized, nearly filling interdental space, sagittal blade in profile nearly as high as long, evenly curved.

Variation. Specimen JRJ_01249, a male from Ngong, Kenya, has exceedingly slender wings (FWL:FWW=4.39, A2 Excel File 2), more so than any other individual of *Tmesibasis* examined. It otherwise matches externally with other *imperatrix* males in almost all anatomical regards, and appears to be merely slightly small overall with its wings anomalously narrow. It was not, however, dissected for analysis of genitalic structures. Another male from Ngong, JRJ_01261, is larger but has normal wing dimensions; a male with wings of comparable length, from Kibwezi, Kenya, JRJ_01252, also has the standard FW length-to-width ratio (FWL:FWW=3.89, A2 Excel File 2). The interior surface of male S9 is only visible in very few unmacerated specimens. JRJ_01268, a female, is treated here tentatively as *imperatrix* on account of several shared features (labrum evenly orangish, wing shape as described below, ectoprocts not produced dorsally), but also has several features of *majesta* and may represent a hybrid condition. Its wings differ from other *imperatrix* females in the following features: FW subapical blotch widely separated from mesal blotch and shortened, not narrowing as it strikes apical area; HW subapical blotch also widely separated from mesal blotch, narrowing slightly before joining apical area; in summary, its wing shape matches *imperatrix*, but its wing pattern matches *majesta*. Further, it exhibits the following *majesta*-like features: its pronotal anterior flange lobes and posterior flange mesal surfaces are darkened, the interdens blade is slightly taller in profile, and the vetrovalvae apices in lateral view are not bulblike.

Primary type.—

Tmesibasis imperatrix van der Weele, 1909. Holotype ♀, BMNH, examined (A2 Fig. 45, 49). *Type locality*: Africa, Kenya, Voi [-3.397310°, 38.555934°], 577 m. *Label data*: “Type /// Voi. 10.V. 97 /// B. E. Africa. C.S. Betton. 98—12. /// Tmesibasis imperatrix Type vdWeele /// imperatrix Weele /// JRJ 01247”. *Condition*: good, right antennae broken off at base, missing. *Notes*: Van der Weele (1909) explicitly indicated that he had seen only one specimen. The locality abbreviation on the holotype label, “B. E. Africa”, is for British East Africa, and the collection year is 1897.

Additional material examined.—*Kenya*: Kahaido [BMNH: 2 ♂♂, JRJ_01249, JRJ_01261 (A2 Fig. 15)]; Kiambu [BMNH: 1 ♂, JRJ_01251 (A2 Figs. 44, 46)]; Nairobi [USNM: 1 ♂, JRJ_1028]; Makueni [BMNH: 1 ♂, JRJ_01252 (A2 Figs. 47, 48)]; Taita Taveta [MNHN: 1 ♀, JRJ_01246]. *Tanzania*: Tanga [MFNB: 1 ♀, JRJ_01006 (A2 Fig. 17, 18, 20)]. *Uncertain locality*: [BMNH: 1 ♀, JRJ_01270 (A2 Fig. 50)]. *Notes*: A specimen bearing incorrectly a “Cotypus” label in Navás’s handwriting (JRJ_01246) was also examined. This specimen was collected in 1912 after *imperatrix* was described, and therefore cannot be a syntype.

Natural history.—Specimens examined were collected at elevations from ca. 230 to 2200 meters.

Discussion.—This species is very similar to *T. majesta* and partially sympatric with it in its southwestern geographic distribution. Most were recorded far inland in south-central Kenya, but a few were found near (<25 km) the coast of Kenya and Tanzania. It can be separated from *T. majesta* on the basis of several features (see identification key, diagnoses and figures for the two species, and 'Discussion' for *T. majesta*, below).

Regarding van der Weele's (1909) selection of the name '*imperatrix*', he provided no explanation, but perhaps its meaning is sufficient. *Tmesibasis imperatrix* has a remarkable appearance, as noted by Navás (1912) who compared it to the species *T. alberti*: "Je me permets d'appeler *Alberti*…la plus belle parmi les Ascalaphides holophthalmes que j'aie vus, et non inférieure en beauté à l'*imperatrix*" ['Let me call...*Alberti* the most beautiful among the holophthalmine ascalaphids I have ever seen, and not inferior in beauty to *imperatrix*']. Apparently van der Weele also felt the beauty, or at least the patterns, of *T. imperatrix* were akin to that of royalty.

Tmesibasis lacerata *(Hagen)*

(A2 Figs. 25, 29, 51–58, 105)

Ascalaphus laceratus Hagen, 1853

—Hagen 1853 r#444: 481 {OD, TL}; Hagen 1862 r#2749: 92, pl. V fig. 3 {DIS, RD}

Tmesibasis lacerata (Hagen)

—McLachlan 1871 r#353: 242 {DIS, TSP (of *Tmesibasis* n. gen.)}; van der Weele 1909 r#420: 89, fig. 55 {DIS, GD, RD, SR, TL, TR, TS}

Etymology and nomenclatural notes.—*lacerata*: laceratus (Latin), 'to cut'. No reason for the name selection is given in the original description, but it may refer to the sharp appearance of the falcate portion of the wings or the strong petiolation of the wing bases, perhaps contrasted with the well-developed anal process of the FW.

Diagnosis.—Male: mesal blotch with height at least half of width along posterior margin, symmetrically triangular, with no secondary mesal extension of pigment, and usually not contiguous with subapical blotch; blyzocytes 1–2 mesally devoid of pigment, only very rarely filled in; proximal one half to two-thirds of hyaline area with brownish tint. Female: FW length:width < 3.7; HW weakly falcate; mesal blotches tall and well-developed, proximal margins curved toward wing base; HW subapical blotch narrowed considerably where it joins apical blotch.

Distribution (A2 Fig. 105).—Southern Africa: Malawi, Mozambique, Namibia, South Africa, Zambia, Zimbabwe. This species has a somewhat broad distribution and has been collected more than almost any other (a few more specimens were available for *T. waelbroecki*). Although no specimens were examined from Angola or Botswana, *T. lacerata* almost certainly occurs in those countries.

Autapomorphies.—Pronotum anterior flange lobes medially dark brown to black (char. 7, state 1); FW subapical blotch in males tall, separated from both apical and mesal blotches by a gap in pigment (char. 24, state 3); HW mesal blotch in females with its anterior apex separated from the posterior margin of the anterior blotch by only two rows of cells, and the proximal margin recurved proximad (toward wing base) (char. 29, state 3).

Description.—

Size (mm). Male: length of body 21-(25)-28, abdomen 14-(18)-20, forewing 26-(29)-31, hind wing 26-(29)-30, antennae 30-(32)-34. Female: length of body 24-(27)-28, abdomen 15-(18)-21, forewing 32-(33)-35, hind wing 32-(33)-35, antennae 34-(35)-37.

Head. Occiput amber brown. Postorbital sclerite even in width, broadening slightly behind depression of eye, pale brown. Vertex brown. Anterior extra-torular sclerites dark brown, often yellow mesally where they join. Frons brown or amber red, with a small dark brown macula mesally, setae golden yellow. Clypeus unevenly yellowish brown, slightly paler mesally, setae commencing mesally, golden yellow. Labrum orangish brown, setae golden yellow. Paraocular band amber brown, glabrous, but sometimes with some small dark slender brown setae adjacent to ATP. Anterior orbital sclerite sometimes concolorous with paraocular band, but often orange or yellow. Posterior genal triangle concolorous with paraocular band, surface sometimes with short slender brown setae. Mandibles orange to translucent pale brown. Maxillary stipes and palpomeres yellow to amber brown, stipes and palpomere 1 setae brown, palpomere apical whorl setae brown. Submentum, mentum and palpigers yellow, setae yellow; labial palpi amber to reddish brown, setae dark brown; ligula pale amber or orangish. Eyes posteriorly very weakly bilobed. *Antennae.* Scape reddish to dark brown, setae pale yellow with some dark brown setae mixed in laterally. Pedicel distal margin orange or yellow; pore moderately large. Flagellum with 40-43 flagellomeres, including club, whose beginning is indistinguishable, flagellomeres at base of club also difficult to distinguish; color yellowish in basal half, becoming brown in distal half, surface of basal flagellomeres facing eye considerably darkened, apical five to six flagellomeres of club yellow; verticil fringes on basal five to six flagellomeres; setitori somewhat to well-developed in distal half of flagellum. Club poorly distinguished, apical two or three flagellomeres coequal to their width.

Thorax. *Cervix*. Dorsal cervical plates oblong, pale brown, setae golden brown. Cervical sclerite dull yellowish brown, dorsal margin thinly yellow and smooth, anterior setae golden yellow to golden brown. Ventral cervical plate yellow to orangish. *Pronotum*. Length approximately two-fifths that of mesonotum. Pronotum anterior flange lobes brown, anteromesal surfaces darkened, in many specimens as dark as velvety spots, setae brown. Medial transverse band brown, sublaterally and anteriorly pale brown, lateral setae brown; posterolateral knob dorsally pale brown and yellow, lateroventrally dark brown. Posterior flange mesally dark brown and velvety, sagittal line pale brown, sublaterally brown; setae brown. *Mesonotum*. Prescutum subauriculate, sagittal sulcus weak; lobe setae brown. Scutum with velvety spot large, oblong , its long axis directed anterad and slightly oblique toward lateral margins of mesoprescutum and pronotum, often an elongate obscure slightly dark brown stripe positioned laterad of velvety spot and directed toward anterolateral margin of lobe; setae brown. Scutellum posterior swelling bearing a transverse yellow stripe, surface posterad of stripe dark brown; setae brown. Subscutellum mesally yellow, otherwise brown. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum mesally yellow, laterally dark brown. Scutum brown, velvety spot texture well-developed, setae brown. Scutellum sagittal surface with a broad, very diffuse longitudinal pale brown to yellowish stripe, posterior swelling with a transverse yellow stripe, contiguous with sagittal stripe, lateral setae brown. *Pleuron*. Mesanepimeron projection short and often darkened; dorsal margin of mesobasisternum a narrow yellow transverse stripe, ventral surface dark brown; mesothoracic subalar membrane posterior area yellow; setae golden brown.

Legs. *Morphology*. Femora with dorsoapical processes well-developed. *Color patterning*. Coxae more-or-less evenly brown. Trochanters and femora reddish brown to somewhat dark brown, apical process yellow on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color circumscribing tibia at extreme base, but quickly narrowing into a longitudinal posterodorsal stripe that continues to narrow distally. *Chaetotaxy*. Coxae setae golden yellow or golden brown. Trochanters setae brown. Femur setae dense, long, slender, golden yellow, golden brown and brown. Tibia setae somewhat dense, medium long, slender, golden yellow, golden brown and brown.

Wings (A2 Figs. 25, 29, 51–54). *Dimensions and shape*. Long, FW length approximately coequal to that of HW, but apex of HW extending well beyond that of FW in unspread specimens; anterior margins straight or very slightly convex; wing apical angles acute and pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal half, in both wings posterior margin past midpoint very slightly falcate in males, slightly (FW) to distinctly falcate (HW) in females. Wings in females relatively larger and more slender than those of males with similar body size. *Venation*. FW. Subcostal veinlets slightly irregularly spaced, essentially perpendicular to subcosta and parallel to one another, zero to three (usually none or one) instances of bunching, convergence or divergence, or forking. Pterostigma with four to six veinlets; pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking wing margin proximad of inflection point of anterior and posterior margins. Apical area broadest mesally, containing one to three long forked branches/veinlets divided by eight to fifteen somewhat irregular crossveins. Presectoral area with approximately five to nine primary crossveins. Males with bc0 cell(s) entire from R to Mp but completely filled with pigment, bc1, bc2, bc3b, and bc4b supertending Mp, Rs, Rs_2, and Rs_3 respectively, but separated from R by several small irregular cells, anteriorly margined with pigment, bc5c supertending Rs_4, dorsally margined with pigment; females with bc0 cell(s) entire from Mp to R, usually filled with pigment but sometimes only margined with pigment, remaining blyzocytes entire from subtending vein to R, and only very thinly and weakly margined, mostly devoid of pigment, bc2 set with up to two cells, bc3 with up to three cells, bc4 with up four cells, and bc5 set with up to five cells. Rs forked from R approximately one-fourth distance from wing base, with three and sometimes four well-defined anterior forks loosely paralleling R; Rs_4/Rs5 also with several branches; radial+postsectoral areas roughly occupying distal third of wing. Crossvein cu-mp/1r-m robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin, but becoming somewhat irregular and crooked and sometimes difficult to distinguish from crossveins distad of inflection point. Cua forked proximal to Rs origin; cubital area roughly occupying mesal third of posterior half of wing. Cubital triangle prefork domain with nine to twelve crossveins, distal domain with zero to three sometimes forked or irregular crossveins; marginal cell often present, sometimes subdivided by crossveins, frequently allied with one or two paramarginal cells, but these sometimes poorly developed and only Cua_2+Cup prominent. Anal area cells broadening somewhat distally. 1A appearing to strike and robustly fuse with posterior wing margin in narrowest portion of wing, a very weakly-developed small portion forked anteriorly to fuse with Cup. HW. Similar to FW except as follows. Apical area with seven to fourteen somewhat irregular crossveins. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, well-defined and not fused with Mp_1; posterior medial area occupying approximately one-fourth of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with 12-17 very short regular crossveins; distal domain sometimes with a single crossvein, usually lacking; marginal cell and/or paramarginal cell present. Anal area with a single triangular cell near wing base. Cup appearing to not fuse with 1A. 1A fused with Cua posterad of basal Mp_2 fork, 1A+Cua subsequently fused with posterior wing margin at narrowest portion of wing, separating from margin as wing begins to widen again. 2A more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch faintly visible, this distal portion only weakly developed. *Setae*. Costa basal setae golden brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: ventral membranes in costal area, and dorsal and ventral membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, blyzocytes of radial area, and unpigmented distal portion of radial area near apical area. *Color and patterning*. Veins. Color variable, costa yellow, Sc yellow to pale reddish, remaining major longitudinal veins yellow to dark reddish brown, often pale reddish, most remaining veins, veinlets and crossveins pale yellowish or reddish. Membranes. Subcostal veinlets thickly and diffusely margined with reddish brown pigment; apical area blotch with pigment variable, absent in a short distal stripe along wing margin, and a few to several mesal cells often forming a cluster mostly lacking pigment, but sometimes margined or halfway filled; pigment more-or-less completely filling cells in anterior blotch, distal cells of radial area along Sc+R, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), cubital area (HW: posterior medial area) near fork, and basal and distal portions of anal area, including anal process; often mesal cells of anal area and sometimes mesal cells of triangles margined to nearly completely lacking pigment. Male: Basal two-thirds of hyaline portions of both wings smoky reddish brown, tint becoming fainter distally. FW mesal blotch triangular but variable in shape, often as tall as wide, sometimes curved, usually separated from subapical blotch, but sometimes connected by a thin line of pigment; FW subapical blotch somewhat flatly triangular, one-half as tall as mesal blotch, much shorter than wide, sometimes separated from apical blotch by a narrow gap, other times connected by a thin line of pigment; HW mesal blotch shorter than in FW but not considerably flattened, usually separated from subapical blotch, but sometimes connected by a thin line of pigment; HW subapical blotch Similar to FW. Female: Hyaline membranes lacking any color. FW mesal blotch curved triangular, height coequal to or greater than width, usually broadly separated from subapical blotch; FW subapical blotch broadly triangular, half as tall as mesal blotch, much shorter than wide, joining apical blotch but usually narrowing as it does so (exception JRJ_01017); HW mesal blotch similar in size and shape to that in FW, usually broadly separated from subapical blotch (exception JRJ_01015); HW subapical blotch similar in size and shape to that in FW, narrowing before thinly joining apical blotch.

Abdomen. Tergum. T1 membrane somewhat loose, rarely drawn into longitudinal wrinkles or carinae along margins of groove, but sometimes puckering anteriorly; plates dark brown, lateral area often paler with dark spots at bases of setae, membrane and mesal margins of plates yellow, forming a broad stripe. T2 acrotergite membrane yellow to dull brown, appearing as a continuation of T1 stripe. T2 sagittally yellow to orangish or dull brown; posterolateral macula short, crescent-shaped, posterior margin of macula and tergite margined with pale yellow or gray. T3 base color reddish or yellowish brown, anterior margin with small irregular sublateral black maculae immediately posterad of T2 crescents, posterolateral macula one-third to two-thirds of tergite length, elongate narrow triangular; dark brown spots occasionally present at bases of setae. T4 anterolateral and posterosagittal surfaces pale reddish or yellowish brown, anterior margin with small sublateral black maculae immediately posterad of T3 crescents, posterolateral macula very large, dark brown, similar in shape to that on T3 but more robust; dark brown spots sometimes present at bases of setae. T5 patterning similar to that of T4. T6–T8 patterning similar to that of T4 and T5, but posterolateral macula occupying more of the tergite and somewhat more diffuse, surfaces sometimes bearing small diffuse dark brown spots at bases of setae. T9 yellowish to reddish to dark brown. *Sternum.* S1 dull reddish brown. S2 acrotergite arms very slender. S2 reddish brown. S3 brown, posterolateral macula moderately large, diffuse yellow to orangish, sometimes darkened to reddish or even dark brown, sometimes fused with partner sagittally, a small diffuse dark brown spot at base of each seta. S4–S6 similar to S3, sometimes reddish to yellowish brown, sometimes with posterolateral macula, this often dark brown. S7 brown, often with diffuse reddish or yellowish markings, a small diffuse dark brown spot at base of each seta.

Male terminalia (A2 Figs. 55, 56). *Unmacerated specimens.* Ectoprocts somewhat produced dorsally, bulbous, reddish and yellowish brown mesally, dark brown along posterior margin. S9 brown to dark brown, interior surface reddish brown. Pulvini extruding slightly beyond S9 margin, reddish brown. Gonarcus visible between pulvini, color variable, reddish brown or yellowish and dark brown. *Macerated specimens.* Pulvini large, length two-thirds that of gonarcus, two to three times width. Setae long, stiff, brown, co-equal in length on ectoprocts and pulvini. GPC, lateral view: often dorsoventrally high, dorsal and ventral margins parallel or slightly convergent apicad, dorsal surface arched, darkened, pigment fading or even absent in apical third, dorsal margin not notched, parameres brown, apex very slightly more acute; ventral view: width at broadest point coequal to or greater than overall length, narrow at base, laterally rounded, curved and converging from midpoint toward apex, apical portion somewhat acute, apex slightly rounded, wrinkled portion of each paramere one-third to one-half width of entire paramere, darkened or not, orangish or brown; inter-parameral groove slightly broader in apical portion, pelta very pale yellow, inconspicuous.

Female terminalia (A2 Figs. 57, 58). *Unmacerated specimens*. Ectoprocts produced dorsally, bulbous, reddish brown with a dark brown distal margin to completely dark brown. Ventrovalvae dorsally yellowish, ventrally dark reddish brown. Linguella and distivalvae dark reddish brown. *Macerated specimens*. Distivalvae large, height nearly half that of ectoprocts, oblong, well-separated from each other, somewhat spaced below ectoprocts. Ventrovalvae somewhat short, very narrow, apices slightly bulblike, very slightly produced distad and ventrad. Linguella small, membranous, with a transverse narrow patch of short stiff brown setae. Interdental space shape an inverted equilateral triangle; interdens sclerotized base shape a flat diamond, sagittal blade profile short, ovoid.

Variation. JRJ_01008 expresses a few anomalous features: the forehead macula bears a distinct dark cross or plus sign shape; and bc1 is entire from Mp to R. The apical area of some specimens have marginal pigment strongly expressed (e.g, JRJ_01016), whereas others have the pigment only weakly expressed (e.g, FW of JRJ_01015). At least one male has the hyaline membrane almost devoid of tint (JRJ_01010). Specimen JRJ_01273 is similar to *scopsi* in that its HW mesal and posterior blotches are joined, and there is also a thin line of pigment between the subapical and apical blotch, at least in the FW (the HW tips are missing); its mesal blotches, though, are as in *lacerata*, and are not considerably short or flattened as in *scopsi*. The specimen occurs in eastern Zambia where the distributions of *lacerata* and *scopsi* meet. Away from this overlapping geographic area, the phenotypes of the respective species seem more conserved. The interior surface of male S9 is only visible in very few unmacerated specimens. Specimen

JRJ_01005 displays the following slight differences in the genitalia: Ectoproct protuberance slightly shorter, distivalvae slightly smaller, interdens with a small irregular sclerotized portion situated proximally. Most of these differences may be artifacts due to differential clearing.

Primary type.—

Ascalaphus laceratus Hagen, 1853. Holotype, ♂, MFNB, examined (A2 Fig. 53). *Type locality*: Mozambique, Tete [-16.166667°, 33.600000°], 124 m. *Label data*: “Type /// Mozambique Tette Peters S. /// laceratus Hag.* /// 172 /// Tmesibasis M'L. /// lacerata N19/7 /// LECTOTYPE Tmesibasis lacerata ♂ design. J. R. Jones 2013 /// JRJ 01153”. *Condition*: fair, antennae missing; FWs tattered; abdomen missing segments 7-9. *Notes*: Hagen’s original description is brief, makes no explicit type designation, and contains few critical details to enable proper identification of his type specimen. Hagen provided no label data and only one set of a few measurements of his type material (suggesting he examined only a single individual). A specimen from the MFNB bearing a red type label was examined for this study, and seems to be the specimen described by van der Weele (1909) in his monograph and reported by him as the type, based on label data and van der Weele’s physical description. Unfortunately, the specimen is worn and parts are missing (A2 Fig. 52), making corroboration with Hagen’s few details difficult. The body length closely matches that given by Hagen, but the abdomen apex is broken off (van der Weele mentioned this detail) and missing. Hagen gave the antennae length as well, but they are also both missing. And the wings, which are drooping and have the right FW tip torn off, are short of Hagen's wingspan measurement by two millimeters. This last measurement, in particular, is troubling, as it does not seem possible the specimen can have shrunk, even taking into account the droopiness of the wings and the torn wingtip. It may be that Hagen's measurement was inaccurate, or that van der Weele improperly identified the specimen as Hagen's. In absence of better information, however, it seems imprudent to assume van der Weele was in error, or that another specimen representing the type will turn up (Recommendation 73F). For now, the specimen is accepted as Hagen's type, and van der Weele's designation of it as the holotype is also accepted.

Additional material examined.—*Malawi*: Blantyre [USNM: 1 ♀, JRJ_01724 (in TAMUIC)]. *Namibia*: Kavango [MFNB: 1 ♂, JRJ_01009]. *South Africa*: Limpopo [AMGS: 1 ♂, JRJ_01011; FSCA: 2 ♂♂, JRJ_01010, JRJ_01722 (in TAMUIC), 1 ♀, JRJ_01723 (in TAMUIC); UCDC: 1 ♀, JRJ_01005 (A2 Fig. 58)]; Mpumalanga [AMGS: 1 ♀, JRJ_01017 (A2 Fig. 52); FSCA: 3 ♂♂, JRJ_01013 (A2 Figs. 25, 51, 54), JRJ_01014 (A2 Figs. 55, 56), JRJ_01018]; North West [AMGS: 1 ♀, JRJ_01016 (A2 Fig. 57)]. *Zambia*: Eastern [BMNH: 1 ♂, JRJ_01273]; Southern [CAS: 1 ♀, JRJ_01015]. *Zimbabwe*: Bulawayo [AMGS: 1 ♂, JRJ_01008]; Harare [BMNH: 1 ♂, JRJ_01274].

Natural history.—Based on label data of examined material, several adult specimens were collected near lights at night as: "at light", "black light trap", and "thornscrub & riverine light traps". Attractions to lights is also confirmed by the observational accounts given below. Habitat was also recorded as "woodland" and "thorn scrub forest".

As far as can be determined, besides data from labels, to date no more substantial information has been published regarding *lacerata* biology, nor any aspect of the biology of any *Tmesibasis* species. In the course of this project, however, two firsthand accounts of field observations were shared by colleagues who photographed (B. Dupont: A2 Fig. 29) or collected (L. Snyman) adult specimens of *T. lacerata*. They are presented here, with permission.

Snyman (pers. comm., 2013) reported: "I caught [two] specimens on 10 Feb 2012. The habitat is open savanna or bushveld. [As] there are dangerous game on the farm...the light trap was placed on a lawn next to a fence that separated us from the 'wilderness'. February is in the middle of the rainy season in Gauteng. I started the light trap (two 160W tungsten mix bulbs) just before dusk (approx. 18h00) and waited until our dinner, which was at 19h00. Until then there were no Ascalaphidae. When I returned after dinner, the specimens were sitting on the net of the light trap, which was quite strange, since ascalaphids are not known for their calm and docile nature! I went back this year to the exact same spot, with the exact same light trap, but caught no ascalaphids..."

Dupont (pers. comm., 2013) recorded a similar experience: "This owlfly came unnoticed by us, on the canvas of our kitchen tent in Tlopi tented camp, Marakele NP, a little after sunset. We were busy at the time and kept the tent open; when we noticed its presence it could have been there for half an hour. It was motionless all the time, even under flashlights. It was the only specimen we saw. Tlopi camp is on a small lake, surrounded by a small forest with grassy savannah all around, and it was very dry at the time."

Discussion.—*Tmesibasis lacerata* was the first species of *Tmesibasis* to be described, and in many ways its appearance exhibits the classic gestalt for the genus. The wings are neither long and slender nor short and stout; the anal processes are long and very narrow; and the wingtips are slightly falcate with acuminate apices. Most notably, the blotches are large, well formed and usually unfused (and therefore distinct) in both sexes. Males also usually have the hyaline membrane darkened in the proximal two-thirds of the wings. It is one of the few species for which photographs of live specimens are known (Fig. 29).

Tmesibasis larseni *Hölzel*

(A2 Figs. 4, 59–64, 105)

Tmesibasis larseni Hölzel, 1983

—Hölzel 1983.12.30 r#2993: 235, figs. 1–7 {OD, D, DIS, ET, TL, TR, TS}; Hölzel 1998 r#9061: 135 {L}; Sziráki 1998 r#9362: 70 {L}; Sziráki 2000 r#9872 {GD, SR}; Aspöck et al. 2001 r#9847 {L}; Hölzel 2004.09.17 r#11274: 226, Abb. 36, 57, 58 {GD, LIT}

Etymology and nomenclatural notes.—*larseni*: a Latinized noun in the genitive case, named by Hölzel (1983) for Mr. T. B. Larsen of London, a specialist on African butterfly taxonomy and collector of the holotype and paratypes.

Diagnosis.—Very similar to *rothschildi* (antennae with a well formed club; wing apical angles rounded; a distinct gap in pigment along posterior wing margin in posterior portion of apical area blotch; blotches with a granularity on mesal portions of cell membranes; entire hyaline area of males with brownish tint), but differing in the following ways: wings not or only very slightly falcate; mesal blotch weakly developed, not contiguous with subapical blotch; subapical blotch weakly developed and often in two small pieces; abdominal pattern poorly developed, posterolateral macular not distinctly triangular.

Distribution (A2 Fig. 105).—Southern Arabian Peninsula: Oman, Saudi Arabia, Yemen.

Autapomorphies.—No unambiguous autapomorphies were recovered in the cladistic analysis for this species.

Description (information on female extracted from Hölzel 1983).—

Size (mm). Male: length of body 24, abdomen 18, forewing 24-(25)-27, hind wing 24-(25)-27, antennae 27-(29)-31. Female: length of body (not provided), abdomen (not provided), forewing 29-(30)-30, hind wing 29-(30)-30, antennae 30-(30)-30.

Head. Occiput reddish and dark brown. Postorbital sclerite mostly even in width, sometimes broadening very slightly near where pronotal anterior flange lobes meet posterior flange, dull yellow to pale brown. Vertex brown. Anterior extra-torular sclerites reddish brown. Frons reddish or orangish brown, setae brown. Clypeus orangish brown, sublaterally dark brown, mesally pale where it joins labrum, setae commencing sublaterally, denser laterally, brown. Labrum amber to reddish brown, setae brown. Paraocular band color uneven, dull to orangish brown, a fringe of medium long dark brown setae running from mandible to ATP. Anterior orbital sclerite pale orangish. Posterior genal triangle concolorous with ventral portion of paraocular band, bearing some short, slender, golden setae. Mandibles translucent brown. Maxillary stipes and palpomeres amber brown, stipes and palpomere 1 setae brown, palpomere apical whorl setae brown. Submentum, mentum and palpigers pale yellow to dull orangish brown, submentum setae pale yellow, these becoming brown on distal part of mentum and palpigers; labial palpi amber, setae brown; ligula amber to orangish. Eyes posteriorly extremely weakly bilobed, this almost imperceptible in males. *Antennae.* Scape reddish brown, setae pale yellow with many dark brown setae mixed in. Pedicel distal margin orange; pore small. Flagellum in male with 38 flagellomeres, including club, which is somewhat distinct, club in male with 10-11 antennomeres, flagellum more-or-less yellowish, darkening slightly distally, including club, surface of basal flagellomeres facing eye and partially circumscribing flagellomeres brown, nodes pale yellow; verticil fringes on ca. seven basal flagellomeres; setitori poorly-developed to absent. Club shape a somewhat broad spindle.

Thorax. *Cervix*. Dorsal cervical plates ovoid, pale brown, setae pale yellow. Cervical sclerite pale yellow, dorsal margin thin and smooth, anterior setae pale yellow. Ventral cervical plate pale yellowish around its base, with a small amount of reddish brown granular coloration on its dorsal surface. *Pronotum*. Length approximately one-fourth length of mesonotum. Anterior flange lobes brown, mesally slightly darker, setae mixed brown and pale yellow. Medial transverse band mesally brown, sublaterally paler, lateral setae brown; posterolateral knob dorsally narrowly yellowish to pale brown, apically and anteroventrally dark brown. Posterior flange mesally brown, sublaterally paler; setae pale yellow and brown. *Mesonotum*. Prescutum auriculate, anterolateral lobe velvety spot texture only narrowly on anterolateral surface, proximally broadly and diffusely margined with orangish; lobe setae brown and pale yellow. Scutum with velvety spot relatively small, kidney bean-shaped; surface with long and slender mixed brown and pale yellow setae, these becoming whitish anterolaterally. Scutellum posterior swelling bearing a narrow transverse diffuse yellow to pale brown stripe, surface posterad of stripe dark brown; setae golden brown. Subscutellum often completely brown, sometimes mesally diffusely yellow. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum brown. Scutum dark brown, velvety spot texture developed, setae golden brown. Scutellum more-or-less evenly brown, lateral setae golden brown. *Pleuron.* Mesanepimeron projection very short; mesothoracic subalar membrane evenly dark brown; setae golden brown.

Legs. *Morphology*. Femora with dorsoapical processes undeveloped. *Color patterning*. Coxae brown. Trochanters and femora brown. Tibiae ventrally reddish brown to dark brown, proximodorsally diffusely yellow. *Chaetotaxy.* Coxae setae golden brown. Trochanter setae brown. Femur setae dense, long, slender, golden yellow, golden brown and brown. Tibia setae somewhat dense, medium long, slender, yellow, golden brown and brown.

Wings (A2 Figs. 59–62). *Dimensions and shape.* FW and HW absolute length coequal; anterior margins straight; wing apical angles very weakly acute, smoothly curved; FW anal process narrow, elongate and apically subacuminate, terminal cell extending to apex of process, lateral margins of process separate, not fused, in both wings posterior margin past midpoint convex to wing tip, HW sometimes very slightly falcate. *Venation*. FW. Subcostal veinlets usually regularly spaced, but otherwise highly irregular, bunching, converging, diverging, or forking, occasionally with secondary crossveins. Pterostigma with five to seven yellow veinlets; brown pigment absent along Sc+R distad of pterostigma. Sc+R striking posterior wing margin at or slightly proximad of inflection point of anterior and posterior margins. Apical area broadest anteromesally, containing one to four long forked branches/veinlets divided by five to nine somewhat irregular crossveins. Presectoral area with approximately five primary crossveins. Males with bc0 cell(s) entire from R to Mp but anteromesally devoid of pigment, bc1, bc2, bc3b, bc4b, and bc5c supertending Mp, Rs, Rs_2, Rs_3, and Rs_4/Rs_5 respectively and anterolaterally and narrowly margined with pigment, entire to R; females with bc0 cell(s) mesally devoid of pigment, bc1b, bc2, bc3b, bc4b, and bc5c narrowly margined anteriorly and laterally. Rs forked from R approximately one-fourth distance from wing base, with three or four well-defined anterior forks loosely paralleling R;

radial+postsectoral areas occupying approximately one-third of distal part of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp somewhat near to Rs origin, joining Mp_2+Cua_1 at or after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin. Cua forked proximal to Rs origin; cubital area occupying approximately two-fifths of posterior half of wing. Cubital triangle prefork domain with seven to eleven crossveins, distal domain with two to three crossveins; marginal cell present, sometimes divided, sometimes broadly joined to triangle, sometimes only connected by Cua_2+Cup. Anal area cells broadening distally. 1A forked approximately two-fifths to one-half distance from wing base to Cua fork, anterior branch fused with Cup, posterior branch fused with posterior wing margin. HW. Similar to FW except as follows. Mp_2 forked proximal to but somewhat after Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, moderately well-defined and not fused with Mp_1; posterior medial area occupying slightly less than one-third of posterior half of wing. Medial triangle long, apex variable, somewhat short, broad and truncate or otherwise irregular; prefork domain with 13-15 very short regular crossveins; distal domain with zero to one crossveins. Anal area with a single triangular cell near wing base. Cup striking a short and somewhat weakly developed 1A, Cup+1A adjoining posterior wing margin well before narrowest portion of wing, fused with it, separating as wing begins to widen again. 2A more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion, anterior branch only very faintly visible. *Setae*. Costa basal setae yellow; subsequent short stiff black setae arranged in irregular rows in basal third of wing, these becoming more dense in distal two-thirds of wing; anal process bearing some long wispy yellow setae; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: dorsal and ventral membranes in costal area, apical area, pigmented portions of presectoral and radial areas, unpigmented distal portion of radial area near apical area, and most other unpigmented membranes on ventral surface of wing. *Color and patterning*. Veins. Costa and Sc usually pale yellow, sometimes reddish, R reddish brown, most remaining veins, veinlets and crossveins pale yellowish to dark reddish brown. Membranes. Subcostal veinlets margined, pigment becoming denser in cells closest to pterostigma and nearly filling costal area; apical area completely filled with pigment, except absent in a stripe along distal portion of Sc+R, forming a distinct gap, and a few to several mesal cells mesally lacking pigment; pigment more-or-less completely filling cells in anterior blotch, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: basal and distal portions of medial triangle), cubital area (HW: posterior medial area) near fork and along Cua_2 (HW: Mp_{2p}), and anal area, including anal process; proximo-mesal cells of anal area thinly margined or devoid of pigment, disto-mesal cells more thickly margined. Male: Entire area of hyaline portions of both wings smoky reddish brown, except for distal portions of radial area near Sc+R, and also margining basal blotch, mesal blotch, and subapical blotch(es). FW mesal blotch somewhat variable in shape, essentially a small asymmetrical triangle, widely separated from subapical blotch; FW subapical blotch very reduced and usually expressed as a very small proximal and distal irregular triangle, these sometimes narrowly joined, distal portion terminating at Sc+R; HW blotches Similar to FW but mesal blotch slightly more produced. Female: Hyaline membranes lacking color or very slightly tinted. FW and HW blotches as in male.

Abdomen. Tergum. T1 plates brown, membrane dull pale brown. T2 acrotergite dull reddish brown. T2 dorsally dull pale reddish brown, laterally dark brown. T3 dorsally pale reddish brown, laterally dark brown, posterolateral macula diffuse and very poorly developed. T4 surfaces almost completely dark brown, anterolateral and posterosagittal surfaces pale reddish or yellowish brown, posterolateral macula diffuse and very poorly developed, each seta with a small or weakly expressed dark brown spot at its base. T5–T8 with patterning as in T4. T9 dark brown, dorsally paler. *Sternum.* S1 dull pale brown. S2 dull reddish brown. S3–S7 dull dark brown, a small dark brown spot at base of each seta. In males, S8 as in previous sternites.

Male terminalia (A2 Figs. 63, 64). *Unmacerated specimens.* Ectoprocts short, dorsally slightly produced, proximally reddish brown and orange, otherwise dark brown. S9 dark brown, interior surface not visible. Pulvini barely visible, dark reddish brown. Gonarcus barely visible, dark brown. *Macerated specimens.* Pulvini length slightly longer than half that of gonarcus, two times width. Setae medium long, stiff, dark, coequal on S9, ectoprocts, and pulvini. GPC, lateral view: length medium short, basally only moderately broad, dorsal and ventral margins parallel, dorsal surface weakly arched, strongly darkened, pigment absent in apical third, dorsal margin subapically distinctly notched, parameres dark brown, apex slightly more acute; ventral view: width at broadest point slightly narrower than overall length, overall shape triangular, base only very slightly narrowed if at all, lateral margins converging toward apex in a shallow curve, apex subacute, wrinkled portion of each paramere one-half width of entire paramere, entire paramere darkened, brown; inter-parameral groove slightly broader in apical portion, pelta pale brown, conspicuous.

Female terminalia. Ectoproct only slightly produced dorsally, not bulbous. Distivalvae relatively large, round, very proximate to ectoprocts. Ventrovalvae short, spaced somewhat from distivalvae, in lateral view apices not protruding distad or ventrad, apex and lateral surfaces bearing numerous setae. Linguella short, interdental space and interdens uncertain.

Variation.—No additional variation was observed beyond that described above.

Primary types.—

Tmesibasis larseni Hölzel, 1983. Holotype by original designation, ♂, BMNH, examined (A2 Figs. 60, 61, 63, 64). *Type locality*: Oman, Dhofar [17.105278°, 54.071111°], 194 m. *Label data*: "OMAN DHOFAR AIN JARSIS 5 x 1979 LEG. T. B. LARSEN /// Holotype ♂ Tmesibasis larseni H. Hölzel 1983 /// JRJ_01306". *Condition*: good, no parts missing; abdomen base missing, abdomen apex dissected, in glycerin. Paratypes, 1 ♂, 1 ♀, NHMB, not examined. *Type locality*: Oman, Dhofar [17.105278°, 54.071111°], 194 m. *Label data*: "OMAN DHOFAR AIN JARSIS 5 x 1979 LEG. T. B. LARSEN". *Condition*: unknown. Paratype ♀, NHMB, not examined. *Type locality*: Saudi Arabia, Gizan [16.883663°, 42.564783°], 194 m. *Label data*: "Saudi Arabia, Gizan, 23.II.1979. A.S. Talhouk". *Condition*: unknown. *Notes*: Hölzel (1983) indicated that his type material was in the BMNH (not seen during 2011 visit), the Naturhistorisches Museum Basel [Switzerland] (NHMB), and his personal collection (now mostly in Vienna: NMW; not included with loan material obtained in 2011).

Additional material examined.—Yemen: Al Hudaydah [HNHM: 1 ♂, JRJ_01019 (A2 Fig. 59)].

Natural history.—No information available.

Discussion.—This species is smaller and has more subdued features than all others in the genus. Its wings show only the slightest hint of falcation, and its wingtips are curved and not strongly acuminate posteriorly. Its blotches are also poorly developed. It is one of only two extant genera (with *Ascalaphus* Fabricius: see Hölzel 1983, Sziráki 1998) known to occur in both Africa and the southern Arabian Peninsula.

Tmesibasis majesta *n. sp.*

(A2 Figs. 6, 9, 11b, 23, 24, 28, 35, 65–72, 99, 105)

Etymology.—from *magister* (Latin), 'chief, administrator', ='majestic'; adjectival. This species is named for the majestic appearance of its wing blotches, which strongly resemble those of *T. imperatrix*.

Diagnosis.—Similar to *imperatrix* (males with slender wings lacking brownish tint in hyaline membrane, and blotches reduced; females with long, slender, highly falcate wings, HW subapical blotches expanded to meet apical blotch, these not or only very slightly narrowed distad of midpoint), but differing as follows. Labrum pale to yellow in basal third, brown to dark brown in distal two-thirds; pronotal anterior flange lobes and posterior flange distinctly darkened medially. Male: FW mesal blotch base very short, broadly triangular, mesal peak produced, broad, elongate, and often curved proximad; HW mesal and subapical blotches usually widely separated from one another, gap approximately equal to height of mesal blotch. Female: apical area broadest mesally, HW apex margin obtusely angled to anterior margin; HW subapical blotch broad band, separated from mesal blotch by a gap equal to or greater than height of subapical blotch.

Distribution (A2 Fig. 105).—Coastal Kenya and Tanzania.

Autapomorphies.—Eye with posteromesal transverse depression (char. 2, state 0); antennal basiposterior surface darkened on first 7+ flagellomeres, and often along entire length, or nearly so, of flagellum (char. 5, state 2); pronotum anterior flange lobes medially dark brown to black (char. 7, state 1); FW mesal blotch in males with anteromedial portion offset from basal portion, broad, elongate, and often curved proximad (char. 23, state 2); interdens outline in lateral view curved (at base), apex secondarily narrowed and subrectangular (char. 39, state 4).

Description.—

Size (mm). Male: length of body 24-(26)-28, abdomen 16-(18)-19, forewing 31-(32)-33, hind wing 32-(33)-33, antennae 37-(40)-42. Female: length of body 27-(28)-29, abdomen 19-(19)-19, forewing 37-(38)-38, hind wing 39-(39)-40, antennae 44-(45)-46.

Head (A2 Fig. 6). Occiput yellowish brown. Postorbital sclerite approximately even in width, broadening very slightly behind depression of eye and again adjacent to dorsal cervical plate, pale brown. Vertex dark orangish brown, mesal surface of each lobe often darker brown. Anterior extra-torular sclerites brown to dark brown, occasionally paler along distal margin. Frons brown or orangish, setae brown or golden brown. Clypeus orangish brown, slightly paler mesally, setae commencing mesally, golden brown. Labrum dark brown, sometimes orangish, paler yellow near clypeus, setae brown. Paraocular band dark to orangish or yellowish brown, glabrous, sometimes a few slender short appressed brown setae adjacent to ATP. Anterior orbital sclerite sometimes concolorous with paraocular band, but often orange or dull yellow. Posterior genal triangle concolorous with paraocular band. Mandibles orangish brown to dark brown. Maxillary stipes and palpomeres yellow to orangish, stipes and palpomere 1 setae brown and golden brown, palpomere apical whorl setae brown. Submentum, mentum and palpigers yellow, setae yellow and brown; labial palpi yellow, darkening in distal palpomeres, setae brown; ligula pale yellow, sometimes mesally dark brown. Eyes round, posteromesal depression essentially absent, only very weakly expressed in a few specimens. *Antennae.* Scape orangish to brown, setae mixed pale yellow and dark brown. Pedicel distal margin orange; pore moderately large. Flagellum with 38-42 flagellomeres, including club, whose beginning is indistinguishable, basal flagellomeres difficult to distinguish; flagellomere anteroventral surfaces yellow in basal half of flagellum, becoming increasingly dark in distal portion of each flagellomere in distal half of flagellum until distal eight to twelve flagellomeres completely dark, posterodorsal surfaces dark, becoming darker in distal half of each flagellomere until flagellum completely dark in distal-most flagellomeres, apical three to four flagellomeres of club yellow; verticil fringes on basal five to six flagellomeres; in males setitori somewhat to well-developed in distal half of flagellum. Club poorly distinguished, apical two or three flagellomeres co- or subequal to their width.

Thorax (A2 Figs. 9, 11b, 67). *Cervix*. Dorsal cervical plates round with texture of golden brown microtrichia, setae golden brown. Cervical sclerite pale yellow, anterior setae yellow. Ventral cervical plate small yellow to orangish. *Pronotum*. Length approximately two-fifths that of mesonotum, setae in paler areas only infrequently with a small reddish brown spot at their base. Anterior flange lobes laterally yellow to brown, distinctly darkened anteromesally, sagittal depression yellow, setae dark brown. Medial transverse band anterolateral margin acute, sometimes drawn into a short peak, mesally dark brown, sublaterally yellow to brown, lateral setae brown; posterolateral knob dark brown distally. Posterior flange yellow in sagittal depression, parasagitally dark brown, sublaterally yellow to brown; setae brown. *Mesonotum*. Prescutum auriculate, sagittal sulcus weak, mesal margin of velvety texture margined with diffuse yellow stripe; lobe setae brown. Scutum with velvety spot large, oblong, its long axis directed anterad and slightly oblique toward lateral margins of mesoprescutum and pronotum, velvety spot often thinly margined with yellow; setae brown. Scutellum posterior swelling bearing a transverse yellow stripe, surface posterad of stripe often dark brown; setae brown. Subscutellum dull yellow to brown. Postnotum sagittal depression yellow, otherwise brown. *Metanotum*. Paraprescutum brown. Prescutum mesally yellow, laterally dark brown. Scutum brown, velvety spot texture well-developed, setae brown. Scutellum sagittal surface with a broad, very diffuse sagittal pale yellow stripe; lateral setae brown. *Pleuron*. Mesanepimeron projection short; subalar membrane posterior area yellow; setae golden brown.

Legs. *Morphology*. Femora with dorsoapical processes well-developed.Tibial spurs and tarsal claws robust. *Color patterning*. Coxae yellowish or orangish to dark brown. Trochanters and femora reddish brown to somewhat dark brown, apical process yellow dorsally along margin and on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color circumscribing tibia at extreme base, but quickly narrowing into a longitudinal posterodorsal stripe that continues to narrow distally. *Chaetotaxy*. Coxae setae golden yellow or golden brown. Trochanter setae brown. Femur setae dense, long, slender, golden brown and brown. Tibia setae somewhat dense, medium long, slender, golden brown, brown, and dark brown.

Wings (A2 Figs. 23, 24, 28, 65, 66, 68, 99). *Dimensions and shape*. Long, FW length coequal to or often very slightly less than that of HW; FW slightly broader and less falcate than HW; anterior margins straight or very slightly convex; wing apical angles acute and pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal half, in both wings posterior margin past midpoint somewhat to highly falcate in most specimens, more so in HW and more so in females. Wings in females relatively larger than those of males, wings of males much more slender. *Venation*. FW. Subcostal veinlets slightly irregularly spaced, essentially perpendicular to subcosta and parallel to one another in basal half, gradually becoming slightly inclined distad in distal half, zero to four (usually just one or two) instances of bunching, convergence or divergence, or forking. Pterostigma with four to six veinlets; pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking wing margin proximad of inflection point of anterior and posterior margins along posterior margin. Apical area broadest mesally, containing one to three long forked branches/veinlets divided by six to fourteen somewhat irregular crossveins. Presectoral area with approximately seven to ten primary crossveins. Males with bc0 cell(s) often entire from R to Mp and completely filled with pigment, rarely mesally pale, bc1, bc2, bc3b, and bc4c supertending Mp, Rs, Rs_2, and Rs_3 respectively but separated from R by several small irregular cells, blyzocytes only anteriorly margined, bc5c supertending Rs4, rarely separated from R by several small irregular cells, dorsally margined with pigment; females with bc0 cell(s) entire from Mp to R, completely filled with pigment or mesally pale, bc1, bc2, bc3b, bc4b, bc5e usually entire from subtending vein to R, but sometimes separated by several small irregular cells, anteriorly margined, mostly devoid of pigment. Rs forked from R approximately one-fourth distance from wing base, with three to four well-defined anterior forks loosely paralleling R; Rs_4 also with several branches; radial+postsectoral areas roughly occupying distal third of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 either slightly before or after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin, but becoming somewhat irregular and sometimes difficult to distinguish from crossveins distad of inflection point. Cua forked proximal to Rs origin; cubital area roughly occupying mesal third of posterior half of wing. Cubital triangle prefork domain with eight to fourteen crossveins, distal domain with zero to three sometimes irregular crossveins; marginal cell present, frequently allied with a well-developed paramarginal cell. Anal area cells broadening somewhat distally. 1A forked approximately one-third distance from wing base to Cua fork, anterior branch fused with Cup, posterior branch fused with posterior wing margin, terminus often obscured. HW. Similar to FW except as follows. Apical area broader, breadth continuing to posterior margin, with four to fourteen somewhat irregular crossveins. In males, bc0 to bc5 supertending Mp_1, Mp_1, Rs, Rs_2, Rs_3, and Rs_4 respectively, not separated from R by small irregular cells. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 almost to wing margin, terminal portions sometimes difficult to distinguish from crossveins; posterior medial area occupying one-fourth of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with 12-16 very short sometimes bunched crossveins, mesal crossveins not obliterated; distal domain with zero to one crossveins; in males, a single marginal cell present, this contiguous with distal domain, not separated by a crossvein; in females, a single marginal cell present, this contiguous with distal domain, not separated by a crossvein, or marginal cell absent and one paramarginal cell present. Anal area with a few cells near wing base. Cup striking 1A, Cup+1A fused with Cua before narrowest portion of wing base, Cup+1A+Cua subsequently fused with posterior wing margin at narrowest portion of wing, separating from margin as wing begins to widen again. 2A sometimes more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch visible, sometimes faint, this distal portion very short. *Setae*. Costa basal setae brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: ventral membranes in costal area, and dorsal and ventral membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, blyzocytes of radial area, and unpigmented distal portion of radial area near apical area. *Color and patterning*. Veins. Costa and all major longitudinal 'down' veins yellow to dull reddish brown, all 'up' veins a dull to dark reddish brown, all remaining veins, veinlets and crossveins yellowish to dull reddish brown. Membranes. Subcostal veinlets thinly margined with reddish brown pigment; apical area blotch with pigment variable, absent near pterostigma, in a short narrow mesodistal stripe near wing margin, and mesodistally along Sc+R, also a few mesal cells only margined; pigment more-or-less completely filling cells in anterior blotch, basal half of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), sometimes cubital area (HW: posterior medial area) near fork, and basal and distal portions of anal area, including anal process;

many cells, more than in *imperatrix*, only thinly margined in mesal portions of mediocubital area (HW: anterior medial area) proximad of Rs origin and in mesal portions of cubital triangle (HW: medial triangle) and areas appearing more open. Male: Hyaline portions of both wings devoid of reddish brown tint. FW mesal blotch greatly reduced, very flatly triangular in base, always mesally produced, mesal portion approximately one and a half to two cells wide, peak sometimes curved toward wing base, blotch basal width coequal to or slightly greater than blotch height, separated, sometimes broadly, from subapical blotch; FW subapical blotch a very small marginal peak followed by a very thin band of pigment touching apical blotch; HW posterior marginal blotches Similar to FW but mesal blotch slightly more reduced. Female: Hyaline membranes lacking any color. FW mesal blotch large, curved triangular, height coequal to or very slightly greater than width, separated, sometimes broadly, from subapical blotch; FW subapical blotch rising in a smooth slope from margin to apical area, anterodistal portion touching posterior reach of pterostigma but slightly narrowed in one specimen; HW mesal blotch similar in size and shape to that in FW but wider at base, separated from subapical blotch; HW subapical blotch similar in shape to that in FW, but more elongate and narrowing only very slightly before joining apical area.

Abdomen. Tergum. T1 plates dark brown, sagittal depression and mesal margins of plates yellow, forming a broad stripe. T2 acrotergite membrane mesally yellow, appearing as a continuation of T1 stripe. T2 sagittally yellow to reddish or dull brown, appearing as a dull continuation of T1 stripe, laterally brown, posterolateral macula crescent shaped, dark. T3 base color grayish to reddish brown, posterolateral macula approximately one-half to three-fifths length of tergite, elongate triangular, diffuse and somewhat irregular; setae with dark brown spots at their bases. T4 dorsal surface almost completely dark brown, anterolateral and posterosagittal surfaces pale reddish or yellowish brown, posterolateral macula similar to that of T3; setae each with a dark brown spot at its base. T5 patterning as in T4. T5–T8 base color greyish or reddish brown, posterolateral macula diffuse and irregular; each seta with a dark brown spot at its base. T9 brown, mesally paler. *Sternum*. S1 brown. S2 acrosternite arms narrow. S2 pale to dark brown. S3 brown, posterior sublateral macula moderately large, diffuse, orange, with dark brown anterior and posterior borders; dark brown spots at bases of setae. S4 and S5 sometimes with orange or dark brown sublateral maculae similar to S3; S4–S7 brown, a dark brown spot at base of each seta.

Male terminalia (A2 Figs. 69, 70). *Unmacerated specimens.* Ectoprocts only very slightly produced dorsally, dark brown. S9 interior surface orangish yellow to reddish brown. Pulvini extruding very slightly beyond S9 margin, orangish yellow to reddish brown. Gonarcus visible between pulvini, large, dark reddish brown, mesally yellowish. *Macerated specimens.* Pulvini length approximately half that of gonarcus, two times width. Setae long, stiff, co-equal in length on ectoprocts and pulvini. GPC, lateral view: length medium, basally broad, dorsal and ventral margins subparallel, dorsal surface arched, subapically weakly notched, darkened, pigment absent in a small triangle at apex, parameres brown, apex slightly more blunt; ventral view: width at broadest point two-thirds of overall length, overall shape approximately round, base narrowed, lateral margins diverging at immediate base, then evenly curved and converging toward apex,

apex rounded, wrinkled portion of each paramere one-third to one-half width of entire paramere, very slightly darkened, orangish; inter-parameral groove broader in apical portion, pelta yellowish, somewhat conspicuous.

Female terminalia (A2 Figs. 35, 71, 72). *Unmacerated specimens.* Ectoprocts brown. Ventrovalvae brown, apical margins orangish to brown. Linguella and distivalvae brown. *Macerated specimens.* Distivalvae small, height approximately two-fifths that of ectoprocts, globose, well separated from one another, very proximate to ectoprocts. Ventrovalvae only slightly elongate, slightly narrowed, apices somewhat bulblike ventrad but not protruding distad in lateral view. Linguella small, membranous, having paired transversely arranged lobes bearing short stiff brown setae. Interdental space triangular; interdens sclerotized base shape a somewhat large flat diamond, sclerotized dark, nearly filling interdental space, sagittal blade in profile height half of length, subquadrangular.

Variation. Anal process somewhat variable in length and degree of lateral magin fusion. Some specimens with pigmented portions of wings slightly darker (JRJ_01232, JRJ_01233, JRJ_01234); subcostal area pigment of JRJ_01234 very dark. Specimen JRJ_01233 with hyaline membranes having very slight fuscous tint. S3 yellow maculae not visible in all specimens. Male JRJ_01257 with pronotal anterior flange lobes not mesally darkened and HW posterior mesal and subapical blotches weakly connected.

Primary type.—

Tmesibasis majesta n. sp. Holotype by present designation, ♀, BMNH, examined (A2 Figs. 9, 24, 28, 35, 66, 67, 71, 72). *Type locality*: Tanzania, Pwani [-8.345833°, 38.960000°], 346 m. *Label data*: "8°20'45"S: 38°57'36"E Matumbi Highlands R. Mwengei, Ponds Tanzania, Alt. 1050 ft. 21 xi 1989, At UV light /// HOLOTYPE Tmesibasis majesta ♀ design. J. R. Jones 2013 /// JRJ 01234". *Condition*: excellent, no parts missing; FWs slightly dinged mesally; abdomen dissected, in glycerin. *Notes*: The female in the best condition and that best expresses the phenotype was selected as the holotype. The abdomen apex, which was macerated for this study, has been placed in a genitalia vial associated with the specimen.

Additional material examined (paratypes).—*Kenya*: Kilifi [BMNH: 3 ♂♂, JRJ_01254, JRJ_01256 (A2 Fig. 11b), JRJ_01257; USNM: 1 ♂, JRJ_01030 (A2 Fig. 68–70, 99)]; Kwale [BMNH: 1 ♀, JRJ_01268; USNM: 1 ♂, JRJ_1029]. *Tanzania*: Pwani [BMNH: 1 ♂, JRJ_01233, 1 ♀, JRJ_01235]; Tanga [BMNH: 1 ♂, JRJ_01232 (A2 Figs. 6, 23, 65)].

Natural history.—One adult specimen was recorded as collected at a UV light.

Discussion.—It was determined late in this study that some males tentatively identified as *T. imperatrix* (males of *T. imperatrix* were undescribed prior to this study) represent a new species. This species, *T. majesta*, expresses more dramatic body coloration (e.g., the mesal portions of the pronotal anterior flange lobes and posterior flange are darkened in both males and females), has more falcate wingtips (particularly the females), and is consistently slightly larger (by one to two mm in all measurements). The patterns of the wings (see diagnoses and figures for both species) and genitalia, in both sexes, also show subtle but distinct differences from *T. imperatrix*. The GPC of *majesta* is very slightly longer and more apically rounded in ventral view, whereas that of *imperatrix* is slightly shorter and apically more acute. In females of *majesta*, the ventrovalvae are more robust, and the interdental plate is more sclerotized, slightly larger and darker, and has a subtly different shape than that of *imperatrix*.

Tmesibasis majesta appears to be a primarily coastal, low elevation species. All known specimens occur within 35 km of the Indian Ocean, at elevations of ca. 80-550 meters. Across their known distribution, all of the northernly collected specimens are males, while the two females examined were recorded from southcentral Tanzania. Only the male JRJ_01233 occured at same site as the *majesta* females.

Tmesibasis rothschildi *van der Weele*

(A2 Figs. 12, 21, 27, 62, 73–80, 105)

Tmesibasis rothschildi van der Weele, 1907

—van der Weele 1907 r#6137: 256 {OD, ET, TL, TR, TS}; van der Weele 1909 r#420: 91, fig. 57 {RD, GD, SR, TL, TR, TS}

Tmesibasis regia Navás, 1915 **new synonym**

—Navás 1915 r#645: 173 {OD, D, TL}

Tmesibasis andruzzii Navás, 1929 **new synonym**

—Navás, L. 1929 r#859: 354, fig. 1 {OD, D, TL}

Etymology and nomenclatural notes.—*rothschildi*: a Latinized noun in the genitive case, named by van der Weele (1909) for Mr. M. de Rothschild, the collector of the type specimen.

Diagnosis.—Very similar to *larseni* (antennae with a well formed club; wing apical angles rounded; a distinct gap in pigment along posterior wing margin in posterior portion of apical area blotch; blotches with a granularity on mesal portions of cell membranes; entire hyaline area of males with brownish tint), but differing in the following ways: wings slightly falcate; mesal blotch well developed, often contiguous with subapical blotch; subapical blotch well-developed and in a single piece; abdominal pattern well-developed as distinct triangular maculae.

Distribution (A2 Fig. 105).—Kenya, Somalia.

Autapomorphies.—No unambiguous autapomorphies were recovered in the cladistic analysis for this species.

Description.—

Size (mm). Male: length of body 21-(24)-27, abdomen 14-(18)-21, forewing 24-(25)-26, hind wing 23-(24)-26, antennae 25-(28)-30. Female: length of body 25-(25)-25, abdomen 18-(19)-19, forewing 29-(30)-31, hind wing 28-(29)-30, antennae 30.

Head. Occiput amber brown. Postorbital sclerite mostly even in width, broadening very slightly near where pronotal anterior flange lobes meet posterior flange, pale brown. Vertex brown, mesal surface of each lobe darkened. Anterior extra-torular sclerites color variable, dull yellow to dark brown. Frons brown, setae pale yellow. Clypeus orangish brown, mesally pale where it joins labrum, setae commencing sublaterally, denser laterally, brown. Labrum brown to dark brown, proximal hinge often pale yellow, setae brown. Paraocular band color uneven, dull brown to orangish brown, a fringe of medium long dark brown setae running from mandible to ATP. Anterior orbital sclerite concolorous with paraocular band or pale orangish. Posterior genal triangle concolorous with ventral portion of paraocular band, bearing some short, slender, brown setae. Mandibles translucent brown. Maxillary stipes orangish and palpomeres brown, stipes and palpomere 1 setae brown, palpomere apical whorl setae dark brown. Submentum, mentum and palpigers pale yellow to dull orangish brown, submentum setae pale yellow, these becoming brown on distal part of mentum and palpigers; labial palpi brown to dark brown, setae brown; ligula orangish. Eyes posteriorly somewhat weakly bilobed, this almost imperceptible in males. *Antennae.* Scape dark brown, setae pale yellow with many dark brown setae mixed in laterally and posteriorly. Pedicel distal margin orange; pore small. Flagellum with ca. 36 (in male) to ca. 39 (in female) flagellomeres, including club, which is somewhat distinct, club with seven to nine antennomeres in male and 10-11 antennomeres in female, flagellum yellowish in proximal one-third to one-half, darkening to brown or dark brown distally, including club, surface of basal flagellomeres facing eye and partially circumscribing flagellomeres dark brown; verticil fringes on basal eight to ten flagellomeres; setitori poorly-developed to absent. Club shape a somewhat broad spindle, this somewhat truncate apically.

Thorax. *Cervix*. Dorsal cervical plates ovoid, brown, setae yellow. Cervical sclerite dull yellow, dorsal portion smooth, thinly pale to bright yellow, anterior setae yellow. Ventral cervical plate pale yellowish around its base, with a small amount of reddish brown granular coloration on its dorsal surface. *Pronotum*. Length approximately one-fourth length of mesonotum. Pronotal anterior flange lobes base color yellowish to brown, anteromesal surfaces darkened, setae brown. Medial transverse band mesally brown, sublaterally paler, lateral setae brown; posterolateral knob dorsally narrowly yellowish to pale brown, apically and anteroventrally dark brown. Posterior flange mesally brown, sublaterally paler; setae pale yellow and brown. *Mesonotum*. Prescutum auriculate, proximally margined with diffuse yellow; lobe setae brown. Scutum with velvety spot large, oblong; surface with long and slender brown setae, these becoming whitish anterolaterally. Scutellum posterior swelling bearing a transverse yellow to pale brown stripe, this often mesally expanded, surface posterad of stripe dark brown; setae brown. Subscutellum often completely brown, sometimes mesally yellow. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum broadly yellow mesally, laterally brown. Scutum brown, velvety spot texture developed, setae golden brown. Scutellum more-or-less evenly brown, posterior swelling mesally diffusely yellow, posterior surface of swelling dark brown, lateral setae brown. *Pleuron*. Mesanepimeron projection very short; ventral surface of mesobasisternite darker brown; mesothoracic subalar membrane usually evenly dark brown, rarely posterior area yellow; setae golden brown.

Legs (A2 Fig. 12). *Morphology*. Femora with dorsoapical processes undeveloped. *Color patterning*. Coxae brown. Trochanters and femora brown. Tibiae ventrally reddish brown to dark brown, proximodorsally diffusely yellow, prothoracic tibia sometimes with yellow color continuing toward apex. *Chaetotaxy*. Coxae setae golden yellow. Trochanter setae brown. Femur setae dense, long, slender, golden yellow, golden brown and brown. Tibia setae somewhat dense, medium long, slender, pale yellow, golden yellow, golden brown and brown.

Wings (A2 Figs. 21, 27, 62, 73–76). *Dimensions and shape*. Moderately long in males, slightly longer in females, FW length very slightly superequal to that of HW; anterior margins very slightly convex; wing apical angles acute but not pointed, rather, smoothly curved; FW anal process narrow, elongate and apically subacuminate, terminal cell extending to apex of process, lateral margins of process separate, not fused, in both wings posterior margin past midpoint weakly falcate. Wings in females relatively larger and more slender than those of males with similar body size. *Venation*. FW. Subcostal veinlets usually regularly spaced, but otherwise highly irregular, bunching, converging, diverging, or forking, occasionally with secondary crossveins. Pterostigma with four to six veinlets; brown pigment absent along Sc+R distad of pterostigma. Sc+R striking posterior wing margin at or slightly proximad of inflection point of anterior and posterior margins. Apical area broadest anteromesally, containing one to four long forked branches/veinlets divided by five to thirteen somewhat irregular crossveins. Presectoral area with approximately five primary crossveins. Males with bc0 cell(s) entire from R to Mp but completely filled with pigment, bc1, bc2, bc3b, bc4b, and bc5c supertending Mp, Rs, Rs_2, Rs_3, and Rs_4 respectively and anteriorly and narrowly margined with pigment, bc1 sometimes completely filled, bc3 and bc4 at least partially separated from R by several small irregular cells; females with bc0 cell(s) entire from Mp to R, filled with pigment, blyzocyte sets 1, 2, and 5 entire from subtending vein to R, sets 3 and 4 either entire to or separated from R by several small irregular cells, all sets narrowly margined dorsally and sometimes laterally, bc sets 3, 4, and 5 with up to two cells. Rs forked from R approximately one-fourth distance from wing base, with three or four well-defined anterior forks loosely paralleling R; radial+postsectoral areas occupying slightly more than one-third of distal part of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp somewhat near to Rs origin, joining Mp_2+Cua_1 after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin. Cua forked proximal to Rs origin; cubital area occupying approximately one-third of posterior half of wing. Cubital triangle prefork domain with seven to nine crossveins, distal domain with one to three crossveins; marginal cell present, sometimes divided, sometimes broadly joined to triangle, sometimes only connected by Cua_2+Cup. Anal area cells broadening distally. 1A forked approximately two-fifths to one-half distance from wing base to Cua fork, anterior branch fused with Cup, posterior branch fused with posterior wing margin. HW.

Similar to FW except as follows. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, moderately well-defined and not fused with Mp_1; posterior medial area occupying one-fourth of posterior half of wing. Medial triangle long, apex variable, somewhat short, broad and truncate or otherwise irregular; prefork domain with 11-14 very short regular crossveins; distal domain with zero to two crossveins. Anal area with a single triangular cell near wing base. Cup striking a short and somewhat weakly developed 1A, Cup+1A adjoining posterior wing margin well before narrowest portion of wing, fused with it, separating as wing begins to widen again. 2A more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch faintly visible. *Setae*. Costa basal setae white; subsequent short stiff black setae arranged in irregular rows in basal third of wing, these becoming more dense in distal two-thirds of wing; anal process bearing some long wispy golden brown setae; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: dorsal and ventral membranes in costal area, apical area, pigmented portions of presectoral and radial areas, unpigmented distal portion of radial area near apical area, and most other unpigmented membranes on ventral surface of wing. *Color and patterning*. Veins. Costa and Sc usually pale yellow, sometimes reddish, R reddish brown, FW Cua and HW Mp_2 yellowish brown, most remaining veins, veinlets and crossveins pale yellowish to dark reddish brown. Membranes. In males, subcostal veinlets broadly and very diffusely margined, pigment becoming denser in cells closest to pterostigma, in some individuals pigment nearly filling costal area; in females, subcostal veinlets darkly margined with brown pigment, pigment filling cells near pterostigma; apical area completely filled with pigment, except absent in a thin stripe along Sc+R, this stripe broadening in apical two-fifths of apical area and forming a distinct gap, and a few to several mesal cells mesally lacking pigment; pigment more-or-less completely filling cells in anterior blotch, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: basal and distal portions of medial triangle), cubital area (HW: posterior medial area) near fork and along Cua_2 (HW: Mp_{2p}), and anal area, including anal process; proximo-mesal cells of anal area thinly margined or devoid of pigment, disto-mesal cells more thickly margined. Male: Entire area of hyaline portions of both wings smoky reddish brown, except for distal portions of radial area near Sc+R and along subapical blotch, and also margining mesal blotch and basal blotch. FW mesal blotch somewhat variable in shape, base flatly triangular, mesal portion often somewhat more narrowly peaked and curved proximad, sometimes separated but often very narrowly connected to subapical blotch; FW subapical blotch a somewhat narrow band, swelling slightly mesally and apically, terminating at Sc+R; HW blotches slightly variable but more-or-less similar to FW. Female: Hyaline membranes lacking color or very slightly tinted. FW mesal blotch a somewhat tall and lumpy triangle, apex somewhat curved proximad, height slightly less than width at base, separated from subapical blotch; FW subapical blotch as in males but slightly higher; HW blotches similar to FW, but posterior blotches somewhat wider basally and mesal and subapical blotches nearly touching.

Abdomen. Tergum. T1 plates brown, membrane diffusely dull yellowish. T2 acrotergite membrane pale yellowish to dull brown, lateral surfaces brown. T2 with a broad sagittal stripe, this diffuse, dull orangish to yellowish brown, lateral surfaces darker, diffusely brown to dark brown, sometimes darker posterodorsally. T3 dorsally and anterolaterally pale reddish to orangish brown, posterolateral macula diffuse, somewhat elongate, directed obliquely from near pleural membrane toward posterodorsal margin, considerably darkening posterodorsally, sometimes with a diffuse dark sublateral macula on anterior margin; a dark brown spot at bases of each seta. T4 similar to T3 but posterolateral macula slightly broader and more diffuse. T5–T8 as in T4, but dorsal surface often darkening somewhat and posterolateral macula shape somewhat variable. T9 dark brown, mesally reddish. *Sternum*. S1 yellowish or orangish brown to evenly brown. S2 brown. S3 slightly darker brown, posterior margin sometimes with a small diffuse yellow macula near pleural membrane, occasionally also sagittally. S4 similar to S3. S5–S8 slightly darker brown, a small dark brown spot at base of each seta.

Male terminalia (A2 Figs. 77, 78). *Unmacerated specimens*. Ectoprocts dorsally produced, somewhat bulbous, dark brown, often orangish dorsally anterad of expanded portion. S9 dark brown, interior surface very slightly visible, reddish brown. Pulvini sometimes visible, dark reddish brown. Gonarcus barely visible, amber to dark reddish brown. *Macerated specimens*. Pulvini length approximately two-thirds that of gonarcus, two times width. Setae medium long, stiff, dark, co-equal in length on ectoprocts and pulvini. GPC, lateral view: basally somewhat broad, dorsal and ventral margins subparallel, dorsal surface slightly arched, darkened, pigment absent in apical third, in some specimens dorsal margin subapically very slightly notched, parameres brown, apex slightly more blunt; ventral view: width at broadest point much narrower than overall length, base only very slightly narrowed, lateral margins converging toward apex in a smooth shallow curve, apex subacute, wrinkled portion of each paramere one-third to one-half width of entire paramere, darkened, brown; inter-parameral groove slightly broader in apical portion, pelta pale yellow, inconspicuous.

Female terminalia (A2 Figs. 79, 80). *Unmacerated specimens.* Ectoproct produced dorsally, not particularly bulbous, reddish brown with a dark brown distal margin or completely dark brown. Ventrovalvae reddish brown with dark brown apices. Linguella and distivalvae dark brown. *Macerated specimens.* Available specimen with some damage. Distivalvae relatively large, oblong, dark, not well-separated from one another, very proximate to ectoprocts. Ventrovalvae short, spaced slightly from distivalvae, somewhat broad, in lateral view apices only very slightly protruding distad, if at all, but not ventrad. Linguella not large, but somewhat well-developed, transverse, somewhat bilobed, bearing short stiff brown setae. Interdental space shape a medium sized triangle; interdens base not sclerotized, sagittal blade, in profile, longitudinally short, evenly curved, height equal to length, pale.

Variation. Specimen JRJ_01023 with cervical sclerite brown. Specimen JRJ_01271, a female, with apical area pigment touching Sc+R. FW 2A only weakly or not fused to 1A in specimens JRJ_01021, JRJ_01020, and JRJ_01271. Specimen JRJ_01022 HW 3A subterminal posterior branch (also present in other species) well-developed and situated proximal to 2A-3A anastomosis, appearing deceptively as a continuation of 3A. Pleural setae are denser in some specimens than others.

Primary types.—

Tmesibasis rothschildi van der Weele, 1907. Lectotype by present designation, ♂, BMNH, examined (A2 Fig. 75). *Type locality*: Kenya, Maungu, [-3.559114°, 38.749908°], 530 m. *Label data*: "SYN-TYPE /// Maungu. 31. IV. 97 /// B. E. Africa. C.S. Betton. 98—12. /// Tmesibasis rothschildi vdWeele Type /// LECTOTYPE Tmesibasis rothschildi ♂ design. J. R. Jones 2013 /// JRJ 01248". *Condition*: excellent, left antennal club missing; right HW slightly torn. Paralectotype, ♂, MNHN, examined. *Type locality*: Kenya, Turkana, [3.314588°, 35.845791°], 453 m. *Label data*: "MUSEUM PARIS Afrique or. angl au S. au Rodolphe M. de Rothschild. 1905 /// TYPE /// Tmesibasis Rothschildi Type vdWeele. /// Tmesibasis rothschildi ♂ det. J.R.Jones 2011 /// JRJ 01624". *Condition*: good, no parts missing, right FW and HW tips torn, right HW broken at base and barely connected. Paralectotype, ♂ [not ♀!], MNHB, examined. *Type locality*: Kenya, Kau, [-2.483333°, 40.433333°], 3 m. *Label data*: "[mostly illegible, but maybe:] Kau watroho or Hanwatroho 18/IV 01 aVG /// Tmesibasis rothschildi v.d.Weele ♀ Type. /// N. O. Afrika S. Galla v. Erlanger S. G. /// Syn-Type /// JRJ 01024". *Condition*: good, no missing parts; left antennae broken near base but attached with glue, bent; abdomen apex dissected, in glycerin. *Notes*: Despite stating that the species is 'represented by a single male' (he is known to have been ambiguous at times with regards to his type/type series concepts and type specimen designations—see Jones and Oswald 2013), van der Weele (1907) described *T. rothschildi* from three specimens, a male from MNHN (JRJ 01624), on which his description focuses, a male from BMNH (JRJ 01248), and a male from MNHB (JRJ_01024), which he mistakenly identified as a female. Van der Weele made no explicit type designation in his original description nor in his subsequent monograph (1909) of the owlflies. All three specimens were examined in this study. The BMNH specimen is in the best condition and is selected as the lectotype.

Tmesibasis regia Navás, 1915. Holotype ♂, RMCA, examined (A2 Fig. 76). *Type locality*: Kenya, Taita Taveta, [-3.002202°, 38.415692°], 482 m. *Label data*: "TYPE /// MUSÉE DU CONGO Tsavo River (B. E. A.) 20 - V - 1913 Dr. Bayer /// R. DET. D 220 /// Typus /// 00712p /// Tmesibasis regia ♂ Nav. Navás S.J. det /// Lectotypus Tmesibasis regia Navás ♂ design. Bo Tjeder 1977 Terminal structures in glycerol in vial /// Lectotypus Tmesibasis regia Navás ♂ design. Bo Tjeder 1977 Terminal structures in glycerin (label on vial) /// HOLOTYPE Tmesibasis regia ♂ det. J. R. Jones 2013 /// JRJ 01244". *Condition*: good, no missing parts, but body glued together, FWs somewhat tattered; abdomen apex dissected, in glycerin. *Notes*: The specimen noted above precisely matches the locality and measurement data recorded in Navás' original description. Navás did not record the number of specimens he examined, but it seems likely that *T. regia* was based solely on this specimen, which is recognized here as the holotype. See 'Discussion', below, for a justification of the synonymy of *T. regia* with *T. rothschildi*.

Tmesibasis andruzzii Navás, 1929. Holotype, sex not indicated, MSNG, not examined. *Type locality*: Somalia, Middle Shebelle Region, Jowhar [2.780000°, 45.500800°], 108 m. *Label data*: "Africa: Benadir, Giohar, IX, 1923, Dr. Andruzzi". *Condition*: unknown. *Notes*: See 'Discussion', below, for a justification of the synonymy of *T. andruzzii* with *T. rothschildi*.

Additional material examined.—*Kenya*: Isiolo [USNM: 1 ♂, JRJ_01020]; Makueni [BMNH: 1 ♀, JRJ_01271 (A2 Figs. 27, 74)]; Meru [1 ♂, JRJ_01022 (A2. Fig. 12)]. *Somalia*: Galguduud [BMNH: 1 ♂, JRJ_01275]; Lower Shabelle [MHNG: 2 ♂♂, JRJ_01021 (A2 Figs. 21, 73), JRJ_01023 (A2 Figs. 77, 78)]. *Uncertain locality*: [BMNH: 1 ♀, JRJ_01262 (A2 Figs. 79, 80)].

Natural history.—No information available.

Discussion.—*Tmesibasis regia* is placed as a new synonym of *T. rothschildi* based on features of the holotype of *T. regia* (wing size, shape and patterning), which fall within the range of variation of *T. rothschildi*.

Tmesibasis andruzzii Navás is placed as a new synonym of *rothschildi* based on Navás' figure (1929: 354 fig. 1) of *T. andruzzii*, which clearly displays the following diagnostic features of *rothschildi*: (1) broadly contiguous mesal and subapical blotches (this feature was pointed out by Hölzel (1983) who may have seen the type specimen); (2) a well-developed subapical blotch separated from the apical blotch by a pigmentless channel in the posterior portion of the apical area on the distal side of Sc+R (rather than on the proximal side of Sc+R as in other species); (3) a fully formed ovoid apical blotch; (4) a curved wing apex; and (5) an anal process with a rounded, rather than acuminate, apex. These features are supported by the following additional features from Navás' original description: (1) the antennal club is "pyriformi elongata" (only *T. larseni* and *T. rothschildi* are known to have a well-developed club); (2) the measurements Navás provided for body and antennae length agree with those measured in this study for *rothschildi* males; and (3) the locality given for the type specimen (Jowhar, Somalia) falls distinctly within the geographic range of *rothschildi* to the exclusion of all other known species. One anomaly, though, regards the measurement he gives for the hind wing, 29.3 mm. This falls within the range of females examined for this study, but not males (A2 Excel File 2). Navás' figure, however, seems to show the hyaline wing membranes tinted, which indicates a male specimen. It thus appears that he described and figured a single male specimen.

Tmesibasis royi *Tjeder*

(A2 Figs. 14, 81–87, 107)

Tmesibasis royi Tjeder, 1980

—Tjeder 1980 r#309: 401, figs. 1–9, 34 {OD, BIO, D, DIS, ET, HAB, TL, TS, TR}

Etymology and nomenclatural notes.—*royi*: a Latinized noun in the genitive case, named by Tjeder (1980) for Mr. Roy Danielsson, who collected the type specimens.

Diagnosis.—T1 plates completely dark brown; T1 membrane puckering into carinae and forming an anterior triangle. Male: mesal blotches neither tall nor especially short or reduced, and not distinctly triangular; proximal one half to two-thirds of hyaline area with brownish tint. Female: HW weakly falcate; mesal blotch proximal margins nearly straight, not strongly curving toward wing base; subapical blotches expanded to meet apical blotch.

Distribution (A2 Fig. 105).—West Africa: Burkina Faso, Gambia, Nigeria, Senegal.

Autapomorphies.—T1 plates in males completely dark cinnamon brown, with dark spots marking setal bases blending into ground color (char. 31, state 1); T1 mesal membrane in males anteriorly puckered, carinate (char. 32, state 1); GPC dorsal margin outline in lateral view subapically very slightly concave (char. 37, state 1); base of interdens in females moderately narrow (char. 38, state 3).

Description.—

Size (mm). Male: length of body 26-(26)-27, abdomen 17-(18)-18, forewing 28-(28)-28, hind wing 28-(28)-29, antennae 36-(37)-38. Female: length of body 26, abdomen 17, forewing 34, hind wing 34, antennae 38.

Head. Occiput amber red or yellow. Postorbital sclerite even in width, broadening slightly behind depression of eye, pale brown. Vertex brown. Anterior extra-torular sclerites reddish to dark brown. Frons reddish amber to brown, setae golden brown. Clypeus amber to orangish brown, setae commencing mesally, denser laterally, golden brown. Labrum orangish or reddish brown, setae brown. Paraocular band dull to dark amber brown, glabrous. Anterior orbital sclerite concolorous with paraocular band, sometimes paler orangish brown. Posterior genal triangle concolorous with paraocular band. Mandibles pale translucent amber brown. Maxillary stipes and palpomeres amber to yellowish, distal palpomere darker, stipes and palpomere 1 setae golden brown, palpomere apical whorl setae brown. Submentum, mentum and palpigers amber to yellowish, setae mixed golden yellow and brown; labial palpi amber, setae brown; ligula dull amber-reddish or yellowish. Eyes posteriorly weakly bilobed. *Antennae.* Scape dark reddish brown, mesally and ventrally sometimes yellowish, setae pale yellow with some dark brown setae mixed in laterally. Pedicel distal margin orange; pore large. Flagellum with 43-47 flagellomeres, including club, whose beginning is indistinguishable, color pale yellowish to pale orangish in basal half, becoming dark orangish to brown in distal half, surface of basal flagellomeres facing eye considerably darkened, apical three to four flagellomeres of club yellow; verticil fringes on basal nine to ten flagellomeres; in males setitori well-developed in distal half of flagellum. Club poorly distinguished, apical four or five flagellomeres coequal to their width.

Thorax. *Cervix*. Dorsal cervical plates round, pale brown, setae golden brown. Cervical sclerite dull pale yellowish to pale brown, anterior setae yellow. Ventral cervical plate pale brown. *Pronotum*. Length approximately two-fifths that of mesonotum. Pronotum anterior flange lobes brown, anteromesal surfaces evenly brown, setae golden brown. Medial transverse band brown, setae golden brown; posterolateral knob dorsally narrowly yellow to orangish, apically and ventrally dark brown. Posterior flange more-or-less evenly brown; setae brown. *Mesonotum*. Prescutum auriculate; lobe setae brown. Scutum with velvety spot large, oblong, its long axis directed anterad and slightly oblique toward lateral margins of mesoprescutum and pronotum; setae brown. Scutellum posterior swelling bearing a transverse yellow to pale brown stripe, surface posterad of stripe dark brown; setae brown. Subscutellum either evenly brown or mesally yellow and otherwise brown. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum mesally yellow, laterally brown. Scutum brown, velvety spot texture well-developed, setae golden brown. Scutellum sagittal surface with a broad, very diffuse longitudinal pale brown or dull yellowish stripe, posterior swelling with a transverse yellow stripe, lateral setae golden brown. *Pleuron*. Mesanepimeron projection short; dorsal margin of mesobasisternum a narrow paler yellowish brown transverse stripe, ventral surface dark brown; mesothoracic subalar membrane posterior area yellow; setae brown to golden brown.

Legs (A2 Fig. 14). *Morphology*. Femora with dorsoapical processes well-developed. *Color patterning*. Coxae brown to dark brown. Trochanters and femora reddish to somewhat dark brown, apical process yellow dorsally along margin and on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color broad basally but gradually narrowing into a longitudinal stripe that continues to narrow distad, reaching almost to tibia apex on prothoracic leg, barely breaching fascia on other legs. *Chaetotaxy*. Coxae setae golden brown. Trochanter setae dark brown. Femur setae dense, long, slender, yellow, golden yellow, golden brown and brown. Tibia setae somewhat dense, medium long, slender, golden brown and brown.

Wings (A2 Figs. 81, 82). *Dimensions and shape*. Long, FW length coequal to or often very slightly less than that of HW; anterior margins very slightly convex; wing apical angles acute and weakly pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal half, posterior margin past midpoint in FW apically very slightly convex, in HW subapically very slightly falcate and concave, more so in female. Wings in females relatively larger and broader than those of males with similar body size. *Venation*. FW. Subcostal veinlets slightly irregularly spaced, essentially perpendicular to subcosta and parallel to one another, zero to four (usually one to two) instances of bunching, convergence or divergence, or forking. Pterostigma with two to six veinlets; pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking posterior wing margin proximad of inflection point of anterior and posterior margins. Apical area broadest mesally, containing one to three long forked branches/veinlets divided by four to fourteen somewhat irregular crossveins. Presectoral area with approximately four to seven primary crossveins. Males with bc0 cell(s) entire from R to Mp but usually completely filled with pigment, sometimes mesally slightly pale, bc1, bc2, bc3b, and bc4b supertending Mp, Rs, Rs_2, and Rs_3 respectively and usually separated from R by several small irregular cells, only anteriorly margined with pigment, bc5b supertending Rs_4, entire to R, dorsally margined with pigment; in female bc5 set with 3 or four cells. Rs forked from R approximately one-fourth distance from wing base, with three and sometimes four well-defined anterior forks loosely paralleling R; Rs_1 subsequent fork with only a few branches; Rs_4/Rs_5 also with a few branches; radial+postsectoral areas roughly occupying distal third of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 slightly before or after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin, becoming somewhat irregular distad of inflection point. Cua forked proximal to Rs origin; cubital area occupying one-third of posterior half of wing. Cubital triangle prefork domain with eight to twelve crossveins, distal domain with one to three sometimes forked or irregular crossveins; marginal cell often present, sometimes subdivided by crossveins, frequently allied with one or two paramarginal cells, but these sometimes poorly developed and only Cua_2+Cup prominent. Anal area cells broadening distally. 1A forked approximately two-fifths distance from wing base to Cua fork, anterior branch fused with Cup, posterior branch fused with posterior wing margin, terminus often obscured. HW. Similar to FW except as follows. Apical area with four to eleven somewhat irregular crossveins. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, usually well-defined and not fused with Mp_1, sometimes irregular; posterior medial area occupying one-third of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with ten to fifteen very short regular crossveins; distal domain with zero to one crossveins; marginal cell present, sometimes a paramarginal cell present. Anal area with a single triangular cell near wing base. Cup striking a short and weakly developed 1A, Cup+1A fused with Cua at base proximad of narrowest portion of wing, Cup+1A+Cua subsequently fused with posterior wing margin at narrowest portion of wing, separating from margin as wing begins to widen again. 2A more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch visible. *Setae*. Costa basal setae golden brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae golden brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: ventral membranes in costal area, and dorsal and ventral membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, blyzocytes of radial area, and unpigmented extreme distal portion of radial area near apical area. *Color and patterning*. Veins. Costa and Sc yellow to pale reddish, R pale yellow to reddish brown, FW Cua and HW Mp_2 reddish brown, most remaining veins, veinlets and crossveins pale yellowish to dark reddish brown. Membranes. Subcostal veinlets thinly and diffusely margined with reddish brown pigment; apical area blotch with pigment variable, FW: absent near pterostigma and in a stripe along wing margin, also a few to several mesal cells margined, halfway filled, or devoid of pigment, HW: absent near pterostigma and in a short, narrow, distal stripe along wing margin near wing apex, this often fused with pigmentless mesal portion of apical area;

pigment more-or-less completely filling cells in anterior blotch, portions of distal cells of radial area along Sc+R, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), cubital area (HW: posterior medial area) near fork and along Cua_2 (HW: Mp_{2p}), and anal area, including anal process; proximo-mesal cells of anal area thinly margined, disto-mesal cells more thickly margined. Male: Basal half of hyaline portions of both wings weakly smoky reddish brown, becoming fainter distally. FW mesal blotch somewhat variable in shape, asymmetrically triangular with irregular sides, thinly touching subapical blotch; FW subapical blotch asymmetrically and usually triangular, half as tall as mesal blotch, much shorter than wide, connected to apical blotch by a thin line along posterior wing margin; HW blotches Similar to FW, but varying slightly, less produced. Female: Hyaline membranes lacking any color. FW mesal blotch curved triangular, not peaked, height about half width, thinly joined to subapical blotch; FW subapical blotch rising from margin to apical area, anterodistal portion narrowingly slightly before touching posterior reach of pterostigma; HW Similar to FW.

Abdomen. Tergum. T1 membrane loose, often drawn into longitudinal wrinkles or carinae along mesal margins of plates, in dried specimens these often puckering into a small triangle at anterior portion of membrane groove immediately posterad of anterior transverse flange; plates completely dark brown, membrane and sometimes plate mesal margins thinly yellow. T2 acrotergite brown, membrane yellow or dull brown to dark brown, appearing as a continuation of T1 stripe. T2 sagittally yellow to orangish or dull brown, anterolaterally brown, posterolateral macula short, crescent-shaped, posterior margin of macula and tergite margined with pale yellow or gray. T3 base color reddish or yellowish brown, anterior margin with small irregular sublateral black diffuse maculae immediately posterad of T2 crescents, posterolateral macula approximately one-third to two-thirds length of tergite, elongate triangular; a diffuse dark brown spot at base of each seta. T4 mostly brown, anterolateral and posterosagittal surfaces pale reddish or yellowish brown, anterior margin with small sublateral black diffuse maculae immediately posterad of T3 crescents, posterolateral area with a small very dark brown macula with diffuse edges similar in shape to the dorsal-most portion of the crescent on T3, a diffuse dark brown spot at base of each seta. T5 patterning as in T4, but more diffuse and less pronounced. T6–T8 base color brown, posterolateral macula diffuse and poorly expressed, antero- and posterolateral area slightly paler, a diffuse dark brown spot at base of each seta. T9 very short, reddish and yellowish brown. *Sternum*. S1 dull pale brown. S2 brown. S3 brown, a moderately large diffuse sublateral yellow macula positioned near posterior margin and often extending to pleural membrane, sometimes fused with partner sagittally, anterior and posterior edges of macula often diffusely dark brown, macula sometime darkened to brown. S4–S7 brown, a diffuse dark brown spot at base of each seta.

Male terminalia (A2 Figs. 84, 85). *Unmacerated specimens.* Ectoprocts slightly produced dorsally, reddish and yellowish brown mesally, dark brown along posterior margin. S9 reddish brown, interior surface reddish brown. Pulvini short, extruding slightly beyond S9 margin, orangish yellow to reddish or dark brown. Gonarcus visible between pulvini, large, dark reddish brown, mesally yellowish. *Macerated specimens.*

Pulvini length half that of gonarcus, two times width. Setae long, stiff, brown, slightly longer on ectoprocts than pulvini. GPC, lateral view: basally broad, dorsal and ventral margins subparallel, converging apicad, dorsal surface arched, darkened, pigment fading to absent at apex, dorsal margin notched or not, parameres brown, apex slightly more acute; ventral view: width at broadest point very slightly greater than overall length; lateral margin curving and converging slightly and evenly toward apex, straightening slightly subapically, apex acuminate, wrinkled portion of each paramere about one-third overall paramere width, entire paramere orange; inter-parameral groove slightly broader in apical portion, pelta inconspicuous.

Female terminalia (A2 Figs. 86, 87). Unmacerated specimen. Ectoprocts slightly produced and bulbous dorsally, reddish brown with a dark brown distal margin to completely dark brown. Ventrovalvae reddish brown. Linguella and distivalvae reddish brown. Macerated specimen. Distivalvae somewhat large, height nearly half that of ectoprocts, oblong, well-separated from each other, protruding from beneath ventral margin of ectoprocts. Ventrovalvae elongate, narrow, apices produced distad but not ventrad, not especially bulblike. Linguella membranous, bearing short stiff brown setae. Interdental space shape a small inverted equilateral triangle; interdens sclerotized base shape a small transverse rectangle, sagittal blade profile very short longitudinally, high.

Variation. Vertex plates subtle but visible in JRJ_01025. In female, pigment of apical area almost completely absent. Interior surface of male S9 only visible in a few specimens. In single female examined, S3 posterior orange spots not extending to pleural membrane.

Primary types.—

Tmesibasis royi Tjeder, 1980. Holotype by original designation, ♂, MZLU, not examined. *Type locality*: Gambia, West Coast, Kabafita Forest Park, 3.5 km N Brikama [13.296750°, -16.643403°], 36 m. *Label data*: “Gambia, Kabatita Forest Park, 2.2 km NNW Brikama. 5.XI.1977. UTM 28PCK 20–70–. Loc. 27. At light, 19.00–20.00". *Condition*: unknown. Paratype ♂, MZLU, not examined. *Type locality*: Gambia, Lower River, Tendaba [13.437538°, -15.807971°], 21 m. *Label data*: “Gambia, Tendeba Camp. 14.XI.1977. UTM 28PDK 12–85. –. Loc. 12A. At light 18.30–20.30”. *Condition*: unknown.

Additional material examined.—*Nigeria*: Yobe [CAS: 1 ♂, JRJ_01012 (A2 Figs. 84, 85)]. *Senegal*: Kedougou [CIRAD: 1 ♂, JRJ_01025 (A2 Fig. 81); MNHN: 1 ♂, JRJ_01237 (A2 Fig. 83, 86, 87)]; Fatick [MNHN: 1 ♀, JRJ_01239 (A2 Fig. 82)].

Natural history.—Tjeder (1980) noted that the type and paratype specimens were collected at light. He described the holotype habitat as “dense savannah forest, surrounded by more open cultivated forests”, and the paratype habitat as “rather scattered savannah near the River Gambia”. Both specimens were caught in the month of November.

Discussion.—Tjeder’s (1980) description of the type series is very thorough and includes large detailed photographs of each specimen, as well as figures of the genitalia, all of which (particularly the wing patterning) enabled confident matching of the specimens examined in this study.

The specimens examined in this study seem cohesive but do exhibit some slight variations in the shapes of the wing blotches, perhaps a result of regional differences attributable to their relatively vast distribution across western Africa. Only *waelbroecki* is also known from this part of the continent (and only *waelbroecki* has a broader known distribution—see Figs. 104, 105). Several of the records of *T. royi* plotted on the distribution map (A2 Fig. 105) are based on images and label data made available by colleagues (e.g., A. Prost, pers. comm.).

Tmesibasis scopsi *Navás*

(A2 Figs. 11a, 16, 30, 88–91, 104)

Tmesibasis scopsi Navás, 1933

—Navás 1933.10.15 r#933: 308, fig. 88 {OD, DIS, ET, TL}

Etymology and nomenclatural notes.—*scopsi*: a Latinized noun in the genitive case, named by Navás (1933) in homage to Ch. Scops, “inventeur” of the type specimen.

Diagnosis.—Male: HW mesal blotch height ca. one-fourth width; FW mesal blotch asymmetrically triangular; mesal and subapical blotches connected by at least a thin line of pigment; gap along margin of wings between subapical and apical blotches also connected by at least a thin line of pigment; membrane of blyzocyte 2 mesally devoid of pigment, only occasionally somewhat filled in; proximal one half to two-thirds of hyaline area with brownish tint. Female: unknown.

Distribution (A2 Fig. 104).—Central east Africa: Democratic Republic of the Congo, Malawi, Tanzania.

Autapomorphies.—FW mesal blotch of males short, height approximately one-fourth width along wing posterior margin (char. 22, state 2).

Description.—

Size (mm). Male: length of body 25-(26)-27, abdomen 18-(19)-19, forewing 26-(28)-30, hind wing 26-(29)-30, antennae 31-(34)-36. Female: unknown.

Head. Occiput brown. Postorbital sclerite even in width, broadening very slightly behind depression of eye, pale brown. Vertex brown. Anterior extra-torular sclerites reddish to dark brown, often pale yellow along distal margin. Frons brown or orangish, setae golden brown. Clypeus orange to reddish brown, setae commencing mesally, denser laterally, golden brown. Labrum orangish or reddish brown, setae brown. Paraocular band reddish to dull yellowish brown, glabrous. Anterior orbital sclerite often concolorous with paraocular band, sometimes dull orangish brown. Posterior genal triangle concolorous with paraocular band. Mandibles pale translucent to reddish brown.

Maxillary stipes and palpomeres dull reddish brown, stipes and palpomere 1 setae brown, palpomere apical whorl setae dark brown. Submentum, mentum and palpigers orangish brown, setae mixed golden yellow and dark brown; labial palpi orangish brown, setae brown; ligula dull amber-red. Eyes posteriorly weakly bilobed. *Antennae*. Scape orangish to brown, setae pale yellow with some dark brown setae mixed in laterally. Pedicel distal margin orange; pore moderately large. Flagellum with 43 flagellomeres, including club, whose beginning is indistinguishable, color orangish in basal half, becoming dark brown in distal half, surface of basal flagellomeres facing eye slightly darkened, apical three to four flagellomeres of club yellow; verticil fringes on basal nine to ten flagellomeres; in males setitori somewhat to well-developed in distal half of flagellum. Club poorly distinguished, apical two or three flagellomeres coequal to their width.

Thorax (A2 Fig. 11a). *Cervix*. Dorsal cervical plates round, brown, setae golden brown. Cervical sclerite dull yellowish brown, dorsal margin narrowly yellow, anterior setae yellow. Ventral cervical plate yellow to dull orangish. *Pronotum*. Length approximately two-fifths that of mesonotum. Pronotum anterior flange lobes brown, anteromesal surfaces in some specimens darkened, sometimes as dark as velvety spots, in other specimens evenly brown, setae brown. Medial transverse band brown, setae brown; posterolateral knob dorsally narrowly yellowish to dull grey, apically and ventrally dark brown. Posterior flange variable, generally evenly brown, sometimes parasagittally dark brown; setae brown. *Mesonotum*. Prescutum auriculate, sagittal sulcus often thinly pigmented, pale or dark; lobe setae brown. Scutum with velvety spot large, oblong, its long axis directed anterad and slightly oblique toward lateral margins of mesoprescutum and pronotum; setae brown. Scutellum posterior swelling bearing a transverse yellow to pale brown stripe, surface posterad of stripe often dark brown; setae brown. Subscutellum either evenly brown or mesally yellow and otherwise brown. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum mesally yellow, laterally dark brown. Scutum brown, velvety spot texture well-developed, setae brown. Scutellum sagittal surface with a broad, very diffuse longitudinal pale brown or dull yellowish stripe, posterior swelling with a transverse yellow stripe, lateral setae brown. *Pleuron*. Mesanepimeron projection short. dorsal margin of meso- and metabasisternum a narrow yellow transverse stripe, ventral surface dark brown; mesothoracic subalar membrane posterior area yellow; setae brown.

Legs (A2 Fig. 16). *Morphology*. Femora with dorsoapical processes well-developed. *Color patterning*. Coxae brown to dark brown. Trochanters and femora reddish to somewhat dark brown, apical process yellow dorsally along margin and on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color circumscribing tibia at extreme base, but quickly narrowing into a posterodorsal longitudinal stripe that continues to narrow distad. *Chaetotaxy*. Coxae setae golden brown. Trochanter setae brown. Femur setae dense, long, slender, golden brown and brown. Tibia setae somewhat dense, medium long, slender, golden brown and brown.

Wings (A2 Figs. 88, 89). *Dimensions and shape.* Long, FW length coequal to or often very slightly less than that of HW, but apex of HW extending well beyond that of FW in unspread specimens; anterior margins very slightly convex; wing apical angles acute and pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal half, in both wings posterior margin past midpoint somewhat falcate in most specimens. Wings of females unknown. *Venation*. FW. Subcostal veinlets slightly irregularly spaced, essentially perpendicular to subcosta and parallel to one another, zero to four (usually one to two) instances of bunching, convergence or divergence, or forking. Pterostigma with four to six veinlets; pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking posterior wing margin proximad of inflection point of anterior and posterior margins. Apical area broadest mesally, containing one to three long forked branches/veinlets divided by six to eleven somewhat irregular crossveins. Presectoral area with approximately five to seven primary crossveins. Males with bc0 cell(s) entire from R to Mp but completely filled with pigment, bc1, bc2, bc3c, and bc4b supertending Mp, Rs, Rs_2, and Rs_3 respectively but separated from R by several small irregular cells, usually only anteriorly margined with pigment, bc5b supertending Rs_4, entire to R, dorsally margined with pigment; females unknown. Rs forked from R approximately one-fourth distance from wing base, with three and sometimes four well-defined anterior forks loosely paralleling R; Rs_4/Rs_5 also with several branches; radial+postsectoral areas roughly occupying distal third of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 usually well after Cua fork but occasionally slightly before (JRJ_01245); Mp_2+Cua_1 paralleling Mp_1 to wing margin, but becoming somewhat irregular and crooked and sometimes difficult to distinguish from crossveins distad of inflection point. Cua forked proximal to Rs origin; cubital area occupying slightly less than one-third of posterior half of wing. Cubital triangle prefork domain with seven to eleven crossveins, distal domain with one to four sometimes forked or irregular crossveins; marginal cell often present, sometimes subdivided by crossveins, frequently allied with one or two paramarginal cells, but these sometimes poorly developed and only Cua_2+Cup prominent. Anal area cells broadening distally. 1A appearing to strike and robustly fuse with posterior wing margin approximately one-third to two-fifths distance from wing base to Cua fork, a very weakly-developed small portion forked anteriorly to fuse with Cup. HW. Similar to FW except as follows. Sc+R striking wing margin well before inflection point of anterior and posterior margins along posterior margin. Apical area with five to nine somewhat irregular crossveins. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, well-defined and not fused with Mp_1; posterior medial area occupying one-fourth of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with ten to fifteen very short regular crossveins; distal domain with zero to two crossveins; marginal cell present, sometimes one or more paramarginal cells present. Anal area with a single triangular cell near wing base. Cup striking a short and weakly developed 1A, Cup+1A fused with Cua at base of narrowest portion of wing, Cup+1A+Cua subsequently fused with posterior wing margin at narrowest portion of wing, separating from margin as wing begins to widen again. 2A more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch faintly visible. *Setae*. Costa basal setae brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: ventral membranes in costal area, and dorsal and ventral membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, blyzocytes of radial area, and unpigmented extreme distal portion of radial area near apical area. *Color and patterning*. Veins. Costa and Sc yellow to pale reddish, R pale yellow to reddish brown, FW Cua and HW Mp_2 reddish brown, most remaining veins, veinlets and crossveins pale yellowish to dark reddish brown. Membranes. Subcostal veinlets thickly and diffusely margined with reddish brown pigment; apical area blotch with pigment variable, FW: absent near pterostigma and in a distal stripe along wing margin, also a few to several mesal cells margined, halfway filled, or devoid of pigment, HW: absent near pterostigma and in a short, narrow, distal stripe along wing margin near wing apex; pigment more-or-less completely filling cells in anterior blotch, portions of distal cells of radial area along Sc+R, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), cubital area (HW: posterior medial area) near fork and along Cua_2 (HW: Mp_{2p}), and anal area, including anal process; proximo-mesal cells of anal area thinly margined, disto-mesal cells more thickly margined. Male: Basal two-thirds of hyaline portions of both wings smoky reddish brown, tint becoming fainter distally. FW mesal blotch somewhat variable in shape, asymmetrically triangular and flattened, thinly touching subapical blotch; FW subapical blotch flatly and symmetrically triangular, half as tall as mesal blotch, much shorter than wide, connected to apical blotch by a thin line along posterior wing margin; HW blotches Similar to FW, but varying slightly, less produced. Female: Unknown.

Abdomen. Tergum. T1 sagittal depression membrane somewhat loose, but only rarely drawn into longitudinal wrinkles or carinae along margins of groove and puckering anteriorly; plates often mostly dark brown, but lateral area frequently paler with dark spots at bases of setae, sagittal depression and mesal margins of plates yellow, forming a broad stripe. T2 acrotergite brown, membrane concolorous with T1 sagittal membrane, yellow to dull brown, appearing as a continuation of T1 stripe. T2 dorsally yellow to orangish or dull brown, laterally brown; posterolateral macula short, crescent-shaped, posterior margin of macula and tergite margined with pale yellow or gray. T3 orangish to dark brown, posterolateral macula approximately one-half to two-thirds length of tergite, elongate triangular, a diffuse dark brown spot sometimes present at bases of setae. T4 orangish to dark brown, anterior margin with small sublateral black diffuse maculae immediately posterad of T3 crescents, posterolateral macula large, diffuse, triangular, a diffuse dark brown spot at base of each seta. T5 patterning as in T4, but more diffuse and less pronounced. T6–T8 orangish to dark brown, posterolateral macula well-developed but with somewhat diffused edges, all surfaces bearing a diffuse dark brown spot at base of each seta. T9 reddish to yellowish brown. *Sternum*. S1 dull yellowish to reddish brown. S2 brown. S3 brown, a moderately large diffuse sublateral yellow macula positioned near posterior margin and extending to pleural membrane, sometimes fused with partner sagittally, posterior and sometimes anterior edges of macula diffusely dark brown, macula sometime darkened. S4 sometimes paler or yellowish posteriorly similar to S3, otherwise S4–S7 brown, a diffuse dark brown spot at base of each seta.

Male terminalia (A2 Figs. 90, 91). *Unmacerated specimens.* Ectoprocts slightly produced dorsally, reddish and yellowish brown mesally, dark brown along posterior margin. S9 reddish brown, interior surface reddish brown. Pulvini medium length, extending beyond S9 margin, reddish brown. Gonarcus slightly visible between pulvini, yellowish and brown. *Macerated specimens.* Pulvini medium length, slightly more than one-half that of gonarcus, two times width. Setae long, stiff, dark, co-equal in length on ectoprocts and pulvini. GPC, lateral view: basally somewhat broad, dorsal and ventral margins subparallel, dorsal surface somewhat arched, darkened, pigment fading or even absent in apical fourth, dorsal margin not notched, parameres brown, apex slightly more acute; ventral view: width at broadest point narrower than overall length; lateral margin basally narrowed, first diverging at base, then converging again at one-third length toward apex, apical portion converging narrowly, acute, wrinkled portion of each paramere half to nearly coequal width of entire paramere, somewhat darkened, brown; inter-parameral groove slightly broader in apical portion, pelta pale yellow, inconspicuous.

Female terminalia. Unknown.

Variation. Type specimen (JRJ_01245) with antennal clubs evenly brown. JRJ_01027 with several anomalous features: cervical sclerite completely dull brown apically; pronotal mesal markings much darker than in other specimens; femur apical dorsal processes ventrally brown; meso- and metathoracic tibial spurs very long reaching nearly to midpoint of fifth tarsomere. Interior surface of S9 only visible in one specimen (JRJ_01026). Specimen JRJ_01255, a male, has anomalous mesal blotches: they are tall and narrow and acuminate (height about two-thirds width at base) and curve very slightly proximad. But the other blotches, the genitalia and other features match *scopsi* completely. Specimen JRJ_01242 also has FW mesal blotches somewhat peaked.

Primary type.—

Tmesibasis scopsi Navás, 1933. Holotype by original designation, ♂ (abdomen apex missing), RMCA, examined (A2 Fig. 88). *Type locality*: Democratic Republic of the Congo, Mahagi, [2.308050°, 30.988540°], 468 m. *Label data*: "MUSEE DU CONGO Mahagi 1931 Ch. Scops /// Tmesibasis scopsi Nav. P. Navás S. J. det. /// R. DET. R 2426 /// Tipo /// TYPE /// Holotypus /// 00713p /// JRJ_01245". *Condition*: good, right prothoracic tarsal claw missing; thorax ventrally attached to pin with gelva glue; left HW posterior margin with a slight ding; abdomen base dorsally cracked and eroding, apex of the abdomen following fourth segment absent. *Notes*: As with many of Navás' descriptions, he appears to have characterized this species from a single specimen (he provides only a single measurement for the forewing and hind wing). A specimen in the RMCA was examined that bears a red type label and was identified by Navás as *T. scopsi*. It also bears a locality label that matches the locality data, date and collector provided by Navás. This specimen is taken to be the holotype of *T. scopsi*. The apex of the abdomen may have been removed for dissection, perhaps by Tjeder, but it now appears to be lost. The specimen is a male, based on length of the antennae, which are much longer than the wings, and the slight tint of the wing membranes. The holotype also matches other known males of *T. scopsi* in size, wing shape and patterning.

Additional material examined.—*Malawi*: Lindi [BMNH: 1 ♂, JRJ_01267 (A2 Fig. 89)]; Morogo [BMNH: 1 ♂, JRJ_01269]; Mtwara [UCDC: 1 ♂, JRJ_01026 (A2 Figs. 90, 91)]; Shinyanga [BMNH: 1 ♂, JRJ_01255]. *Tanzania*: Nkata Bay [RMCA: 1 ♂, JRJ_01242]; Thyolo [CAS: 1 ♂, JRJ_01027]. *Uncertain locality*: [BMNH: 1 ♂, JRJ_01266].

Natural history.—Unknown.

Discussion.—Tjeder (1980) noted a strong morphological similarity between *T. scopsi* and *T. royi*. However, the characters he used to differentiate them seem to be highly variable and therefore unreliable for species diagnosis. For example, he stated that *T. scopsi* had a brown antennal club, while that of *T. royi* is terminally yellow. But in the specimens examined for this study (only 8), only the type specimen had a completely brown club (among all *Tmesibasis* species only *T. scopsi* was observed to vary in this trait). Tjder stated that only *T. scopsi* has the “black ventral stripe on the proximal flagellar segment”, but, in this study, both *T. scopsi* and *T. royi* exhibited this feature. And he suggested that *T. scopsi* has broader wings. But ratios of forewing length to width in males (A2 Excel File 2) show broad overlap for the two species (*T. royi*: 3.37–3.67; *T. scopsi*: 3.22–3.56). Better features for distinguishing these species include geography (*T. royi* is a western species and *T. scopsi* eastern), T1 membrane expression (puckered and carinate in *T. royi* [A2. Fig. 83], not puckered nor carinate in *T. scopsi*) and T1 plates coloration (completely dark in *T. royi* [A2 Fig. 83], laterally paler in *T. scopsi*) and the FW mesal blotch shape in males (tall with ragged sides in *T. royi* [A2 Fig. 81], short with more-or-less straight sides in *T. scopsi* [A2 Fig. 88]).

Tmesibasis scopsi males also strongly resemble those of *T. lacerata* and *T. alberti*, but the flattened posterior blotches and central-east distribution of the latter two species set them apart from *T. scopsi*. No examined female *Tmesibasis* specimens were matched to *T. scopsi* in this study. A photograph of a female that may represent *T. scopsi* was captured in Gorongosa National Park, Mozambique (A2 Fig. 30), where the distribution ranges of *T. scopsi* and *T. lacerata* meet (A2 Figs. 104, 105). Its wing shape and patterns resemble those of *T. lacerata* but differ in that the HW mesal blotch is shorter, and its proximal margin is not strongly recurved toward the wing base.

Tmesibasis simplex *n. sp.*

(A2 Figs. 92–95, 104)

Etymology.—from *simplex* (Latin), 'single, simple, not complex'; adjectival. This species is named for the overall smaller number of cell rows and cells in the wings than in other species.

Diagnosis.—Male: FW cubital area with only ca. eight cell rows between Cu2A and Mp1 meeting the wing posterior margin (though a few cells within rows may be divided); blyzocyte sets 2–5 only thinly margined, voids appearing slightly larger; wings weakly falcate; wing apical angles acute but tips weakly rounded; posterior blotches neither tall nor short; FW mesal blotch asymmetrical; mesal, subapical and apical blotches all at least thinly connected by pigment; entire hyaline area with brownish tint. Female: unknown.

Distribution (A2 Fig. 104).—East Africa: Ethiopia, South Sudan.

Autapomorphies.—Wing venation open, FW cubital area with ca. 7–8 more-or-less complete cells rows meeting wing posterior margin (char. 15, state 1); T1 plates in males completely dark cinnamon brown, with dark spots marking setal bases blending into ground color (char. 31, state 1).

Description.—

Size (mm). Male: length of body 25-(26)-27, abdomen 16-(17)-19, forewing 28-(29)-31, hind wing 28-(29)-31, antennae 36-(36)-36. Female: unknown.

Head. Occiput amber brown. Postorbital sclerite mostly even in width, broadening slightly behind depression of eye, pale brown. Vertex brown. Anterior extra-torular sclerites dark brown, paler along distal margin. Frons orangish brown, setae golden brown. Clypeus orangish brown, setae commencing mesally, denser laterally, golden. Labrum dark brown, laterally orangish brown, setae golden. Paraocular band dull dark brown, becoming pale orangish ventrad of clypeus, glabrous. Anterior orbital sclerite slightly paler brown than paraocular band. Posterior genal triangle concolorous with ventral portion of paraocular band. Mandibles translucent brown. Maxillary stipes and palpomeres orangish, stipes and palpomere 1 setae golden brown, palpomere apical whorl setae dark brown. Submentum, mentum and palpigers orangish, setae mixed golden yellow and dark brown; labial palpi orangish, terminal palpomere orangish or dark brown, setae brown; ligula dull amber-red. Eyes posteriorly somewhat weakly bilobed. *Antennae.* Scape dark brown, setae pale yellow with many dark brown setae mixed in laterally. Pedicel distal margin orange; pore moderately large. Flagellum with 43–45 flagellomeres, including club, whose beginning is indistinguishable, color yellowish in basal half, becoming brown in distal half, darker dorsally, surface of basal flagellomeres facing eye darkened to almost black, apex of club evenly brown; verticil fringes on basal eight to ten flagellomeres; setitori well-developed in distal half of flagellum. Club poorly distinguished, apical two or three flagellomeres coequal to their width.

Thorax. *Cervix*. Dorsal cervical plates not visible. Cervical sclerite evenly dull yellowish brown, anterior setae yellow. Ventral cervical plate pale yellowish around its base, with a small amount of reddish brown granular coloration on its dorsal surface. *Pronotum*. Length approximately two-fifths that of mesonotum. Pronotum anterior flange lobes evenly brown, setae brown. Medial transverse band mesally somewhat dark brown, sublaterally brown, lateral setae brown; posterolateral knob dorsally narrowly yellowish to pale brown, apically and ventrally dark brown. Posterior flange evenly slightly darker brown; setae brown. *Mesonotum*. Prescutum auriculate, sagittal sulcus often thinly pigmented, pale; lobe setae brown. Scutum with velvety spot large, oblong, its long axis directed anterad and slightly oblique toward lateral margins of mesoprescutum and pronotum, an elongate obscure slightly dark brown stripe positioned laterad of velvety spot and directed toward anteromesal margin of lobe; setae brown. Scutellum posterior swelling bearing a transverse yellow stripe, surface posterad of stripe dark brown; setae brown. Subscutellum mesally pale yellowish brown, otherwise brown. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum mesally yellow, laterally brown. Scutum brown, velvety spot texture developed, setae golden brown. Scutellum sagittal surface with a broad, almost inperceptible very diffuse pale brown or dull yellowish stripe, posterior swelling with a transverse yellow stripe, lateral setae brown. *Pleuron*. Mesanepimeron projection short, dark brown. dorsal margin of meso- and metabasisternum a narrow yellow transverse stripe, ventral surface dark brown; mesothoracic subalar membrane posterior area yellow; setae brown.

Legs. *Morphology*. Femora with dorsoapical processes well-developed. *Color patterning*. Coxae brown. Trochanters and femora reddish to somewhat dark brown, apical process yellow dorsally along margin and on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color broad basally but gradually narrowing into a posterodorsal longitudinal stripe that continues to narrow distad. *Chaetotaxy*. Coxae setae yellow. Trochanter setae brown. Femur setae dense, long, slender, golden brown and brown. Tibia setae somewhat dense, medium long, slender, golden brown and brown.

Wings (A2 Figs. 92–93). *Dimensions and shape.* Long, FW and HW absolute length coequal; anterior margins very slightly convex; wing apical angles acute and pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal portion, in both wings posterior margin past midpoint somewhat falcate. Wings of females unknown. *Venation*. FW. Subcostal veinlets slightly irregularly spaced, essentially perpendicular to subcosta and parallel to one another, one to three instances of bunching, convergence or divergence, or forking. Pterostigma with four (only visible in left FW of JRJ_01253) veinlets; pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking posterior wing margin proximad of inflection point of anterior and posterior margins. Apical area broadest mesally, containing one to three long forked branches/veinlets divided by six to nine somewhat irregular crossveins. Presectoral area with approximately four to eight primary crossveins. Males with bc0 cell(s) entire from R to Mp but completely filled with pigment, bc1, bc2, bc3b, and bc4b supertending Mp, Rs, Rs_2, and Rs_3 respectively but at least partially separated from R by several small irregular cells, only anteriorly and narrowly margined with pigment, bc5 supertending Rs_4, entire to R, dorsally very thinly margined with pigment; females unknown. Rs forked from R approximately one-fourth distance from wing base, with three or four well-defined anterior forks loosely paralleling R; Rs_4/Rs_5 with a few branches; radial+postsectoral areas roughly occupying distal third of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 at or slightly after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin. Cua forked proximal to Rs origin; cubital area occupying slightly less than one-third of posterior half of wing. Cubital triangle prefork domain with seven to ten crossveins, distal domain with one to two crossveins; marginal cell present, sometimes subdivided by a crossvein. Anal area cells broadening distally. 1A forked approximately one-third distance from wing base to Cua fork, anterior branch fused with Cup, posterior branch fused with posterior wing margin. HW. Similar to FW except as follows. Apical area with four to seven somewhat irregular crossveins. Mp_2 usually forked well after Rs origin, Mp_{2a} paralleling Mp_1 to wing margin, moderately well-defined and not fused with Mp_1; posterior medial area occupying one-fourth of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with 11-13 very short regular crossveins; distal domain without crossveins; marginal cell present, sometimes a paramarginal cell present. Anal area with a single triangular cell near wing base. Cup striking a short and weakly developed 1A, Cup+1A quickly fused with posterior wing margin well before narrowest portion of wing, separating from margin as wing begins to widen again. 2A weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch faintly visible. *Setae*. Costa basal setae brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae brown. All concave veins, veinlets and crossveins of dorsal surface and all convex veins, veinlets and crossveins of ventral surface with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: ventral membranes in costal area, and dorsal and ventral membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, blyzocytes of radial area, and unpigmented extreme distal portion of radial area near apical area. *Color and patterning*. Veins. Costa and Sc yellow to pale reddish, R reddish brown, FW Cua and HW Mp_2 reddish brown, most remaining veins, veinlets and crossveins pale yellowish to dark reddish brown. Membranes. Subcostal veinlets thickly and diffusely margined with reddish brown pigment; apical area blotch pigment absent in a distal stripe along wing margin, and several mesal cells margined or halfway filled; pigment more-or-less completely filling cells in anterior blotch, portions of distal cells of radial area along Sc+R, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), cubital area (HW: posterior medial area) near fork and along Cua_2 (HW: Mp_{2p}), and anal area, including anal process; proximo-mesal cells of anal area thinly margined, disto-mesal cells more thickly margined. Male: Basal two-thirds (JRJ_01253) to almost complete area (JRJ_01031) of hyaline portions of both wings smoky reddish brown, tint becoming fainter distally. FW mesal blotch somewhat variable in shape, asymmetrically triangular and somewhat flattened, very thinly touching subapical blotch; FW subapical blotch a flattish swelling, less than half as tall as mesal blotch, much shorter than wide, connected to apical blotch by a narrow line along posterior wing margin; HW blotches Similar to FW, but varying slightly, less produced. Female: Unknown.

Abdomen. Tergum. T1 membrane flexible, forming longitudinal carinae or not, but not anteriorly puckering; plates completely dark brown, membrane yellow, glabrous. T2 acrotergite sclerotized portions dark brown, membrane yellow, appearing as a continuation of T1 stripe. T2 posterolateral macula short, crescent-shaped, posterior margin of macula and tergite margined with pale yellowish brown. T3 base color orangish to dark reddish brown, posterolateral macula occupying one-third to two-thirds of tergite, elongate triangular; a large diffuse dark brown spot present at base of each seta. T4 reddish to dark grayish brown, anterior margin with small sublateral black diffuse maculae immediately posterad of T3 crescents, posterolateral macula large, well-developed, quadrangular; a diffuse dark brown spot at base of each seta. T5 patterning as in T4, but more diffuse and less pronounced. T6–T8 grayish brown, pattern as an T5 but more diffuse and poorly expressed, each seta with diffuse dark brown spot at its base. T9 dark brown. *Sternum*. S1 brown. S2 arms thin. S2 brown. S3 brown, a moderately large diffuse sublateral orange macula positioned near posterior margin, posterior and sometimes anteromesal edges of macula diffusely dark brown. S4 posterior margin dark brown, otherwise S4–S7 grayish brown, a large diffuse dark brown spot at base of each seta.

Male terminalia (A2 Figs. 94–95). *Unmacerated specimens.* Ectoprocts slightly produced dorsally, completely dark brown. S9 dark brown, interior surface dark brown. Pulvini short, extruding slightly beyond S9 margin, dark brown. Gonarcus barely visible between pulvini, dark reddish brown. *Macerated specimens.* Pulvini length greater than half that of gonarcus, two times width. Setae long, stiff, dark, co-equal in length on ectoprocts and pulvini. GPC, lateral view: length short, basally somewhat to very broad, dorsal and ventral margins converging apicad, dorsal surface weakly arched, darkened, pigment fading to absent at apex, dorsal margin notched, parameres brown, apex slightly more blunt; ventral view: overall width coequal to overall length; lateral margin converging slightly and in an even curve, becoming straight and converging apically, apex somewhat acute, wrinkled portion of each paramere about one-third overall paramere width, entire paramere orangish brown; inter-parameral groove broader mesally, pelta pale yellow.

Female terminalia. Unknown.

Variation.—The two specimens examined in this study differ in numerous regards. In JRJ_01031, which was selected as the holotype, the T3 lateral margin is highly concaved, the base color of segments four through nine is essentially dark brown, the tergite sublateral maculae are shorter, and the wings are more fully tinted. In the other available specimen, JRJ_01253, an unpublished type of Tjeder, the lateral margin of T3 is not as concave, the sagittal surface of tergites four through nine is paler orangish, the posterolateral macula is somewhat more drawn out anteriorly, and only the proximal two-thirds of the wings are tinted.

Primary type.—

Tmesibasis simplex n. sp. Holotype by present designation, ♂, USNM, examined (A2 Figs. 92, 93). *Type locality*: South Sudan, Eastern Equitoria [4.038333°, 32.845278°], 1849 m. *Label data*: "SUDAN: Gilo at lights 18-27 Oct. 1979 A. L. Armstrong /// HOLOTYPE Tmesibasis simplex ♂ design. J. R. Jones 2013 /// JRJ_01031". *Condition*: good: no missing parts, right antennae broken but with specimen; FW tips torn; abdomen apex dissected, in glycerin. *Notes*: Neither of the two specimens examined are in good condition; the larger specimen, which expresses the phenotype distinctly and has less wear, is selected here as the holotype.

Additional material examined (paratype).—*Ethiopia*: Benishangul-Gumuz Region [BMNH: 1 ♂, JRJ_01253 (A2 Figs. 94, 95)].

Natural history.—One specimen was collected "at lights".

Discussion.—The two specimens examined are united chiefly on the basis of their open wing venation, with reduced number of cell rows. They also match closely, although not perfectly, in the shape of their wings and wing blotches, color of the thorax, wings and abdomen (both have dark T1 plates, an uncommon feature in other species), and shape of the genitalia. They were also collected close to one another geographically, and in a part of Africa wihout other reported species.

Tmesibasis waelbroecki *van der Weele*

(A2 Figs. 5, 7, 8, 10 11c, 13, 19, 22, 32, 34, 96–104)

Tmesibasis waelbroecki van der Weele

—Van der Weele 1909 r#420: 92, fig. 58 {OD, D, ET, TL, TR, TS}

Etymology and nomenclatural notes.—*waelbroecki*: a Latinized noun in the genitive case, named for Mr. Waelbroeck, an avid collector in the Congo region.

Diagnosis.—Both FW and HW strongly falcate; wings broad. Male: mesal, subapical and apical blotches broadly joined; hyaline membranes strongly and completely tinted. Female: mesal and subapical blotches at least thinly joined; subapical and apical blotches broadly joined, but subapical blotch highest mesally and narrowing before joining apical blotch.

Autapomorphies.—Interdens outline in lateral view subrectangular, apex not secondarily narrowed (char. 39, state 3).

Distribution (A2 Fig. 104).—Central African Republic, Côte d'Ivoire, Gabon, Ghana, Kenya, Nigeria, Togo, Democratic Republic of the Congo, Uganda.

Description.—

Size (mm). Male: length of body 20-(25)-28, abdomen 15-(19)-20, forewing 26-(27)-29, hind wing 25-(27)-28, antennae 31-(32)-33. Female: length of body 24-(26)-28, abdomen 15-(18)-19, forewing 30-(31)-33, hind wing 30-(31)-34, antennae 30-(32)-35.

Head (A2 Fig. 5). Occiput brown. Postorbital sclerite mostly even in width, broadening very slightly behind depression of eye, pale brown. Vertex brown. Anterior extra-torular sclerites dark brown, sometimes with a transverse mesal orange or pinkish stripe. Frons orangish brown, setae golden. Clypeus orangish brown, setae commencing mesally, denser laterally, golden. Labrum evenly orangish brown, proximal hinge often pale yellow, setae golden. Paraocular band orange to dull orangish brown, glabrous. Anterior orbital sclerite concolorous with paraocular band or pale orangish. Posterior genal triangle concolorous with ventral portion of paraocular band, sometimes with a few short, slender, golden or brown setae. Mandibles translucent brown. Maxillary stipes and palpomeres orangish, stipes and palpomere 1 setae golden brown, palpomere apical whorl setae dark brown. Submentum, mentum and palpigers orangish, setae golden brown; labial palpi orangish, setae brown; ligula orangish. Eyes posteriorly somewhat weakly bilobed. *Antennae.* Scape dark brown, setae pale yellow with many dark brown setae mixed in laterally. Pedicel distal margin orange; pore medium small. Flagellum with 43–45 flagellomeres, including club, whose beginning is indistinguishable, color yellowish in basal one-half in males, basal three-fourths in females, becoming reddish brown in distal portion, surface of basal flagellomeres facing eye dark reddish brown, apex of club evenly brown; verticil fringes on basal eight to ten flagellomeres; setitori poorly-developed or absent. Club poorly distinguished, flagellomeres gradually shortening until length of apical four or eight coequal to their width.

Thorax (A2 Figs. 7, 8, 10, 11c). *Cervix*. Dorsal cervical plates round, dull brown, setae golden brown. Cervical sclerite pale yellowish to dull brown, dorsal margin narrowly smooth and pale to dull yellow, anterior setae yellow. Ventral cervical plate pale yellowish around its base, with a small amount of reddish brown granular coloration on its dorsal surface. *Pronotum*. Length approximately two-fifths that of mesonotum. Pronotum anterior flange lobes evenly brown, setae brown. Medial transverse band more-or-less evenly brown, a parasagittal and sublateral very diffuse dark brown spot usually present, setae brown; posterolateral knob dorsally narrowly yellowish to pale brown, apically and ventrally dark brown. Posterior flange more-or-less evenly brown; setae brown. *Mesonotum*. Prescutum auriculate, sagittal sulcus sometimes thinly pigmented, pale; lobe setae brown. Scutum with velvety spot large, sub-ovoid, its width slightly greater than in other species; setae brown. Scutellum sagittal line sometimes slightly darkened, posterior swelling bearing a transverse dull yellow to pale brown stripe, surface posterad of stripe dark brown; setae brown. Subscutellum sometimes completely brown, often mesally yellow. Postnotum brown. *Metanotum*. Paraprescutum brown. Prescutum broadly yellow mesally, laterally brown. Scutum brown, velvety spot texture developed, setae golden brown. Scutellum mesal surface with a broad yellow sagittal stripe, this expanding laterally slightly on posterior swelling, lateral setae brown. *Pleuron*. Mesanepimeron projection very short, dark brown; ventral margin of meso- and metakatepisternite and mesokatepimerite sometimes yellow, metanepimerite often with an anteroventral diffuse yellow macula; dorsal margin of meso- and metabasisternum a narrow yellow transverse stripe, ventral surface dark brown; mesothoracic subalar membrane posterior area yellow; setae brown.

Legs (A2 Fig. 13). *Morphology*. Femora with dorsoapical processes well-developed. *Color patterning*. Coxae brown. Trochanters and femora brown, apical process yellow along margin and on ventral surface. Tibiae ventrally reddish brown to dark brown, dorsally yellow, yellow color broad basally but gradually narrowing into a longitudinal dorsal stripe that continues to narrow distad. *Chaetotaxy*. Coxae setae brown. Trochanter setae brown. Femur setae dense, long, slender, golden yellow, golden brown, brown, and dark brown. Tibia setae somewhat dense, medium long, slender, golden brown, brown, and dark brown.

Wings (A2 Figs. 19, 22, 96–99). *Dimensions and shape.* Moderately long in males, slightly longer in females, FW and HW absolute length approximately coequal; anterior margins very slightly convex; wing apical angles acute and pointed; FW anal process extremely narrow, elongate and apically acuminate, terminal cell ending well before apex of process, lateral margins of process fused in distal portion, in both wings posterior margin past midpoint distinctly falcate. Wings in females relatively larger and more slender than those of males with similar body size. *Venation*. FW. Subcostal veinlets usually regularly spaced, but otherwise highly irregular, bunching, converging, diverging, or forking, occasionally with secondary crossveins. Pterostigma with four to six veinlets; brown pigment absent along Sc+R distad of pterostigma for a few cells. Sc+R striking posterior wing margin proximad of inflection point of anterior and posterior margins. Apical area broadest anteromesally, containing one to three long forked branches/veinlets divided by eight to thirteen somewhat irregular crossveins. Presectoral area with approximately five to eight primary crossveins. Males with bc0 cell(s) entire from R to Mp but completely filled with pigment, bc1, bc2, bc3b, and bc4b supertending Mp, Rs, Rs_2, and Rs_3 respectively but at least partially separated from R by several small irregular cells, bc1 usually completely filled with pigment, bc2, bc3b, and bc4b only anteriorly and narrowly margined with pigment, bc5c supertending Rs_4/Rs_5, entire to R, dorsally very thinly margined with pigment, often two cells in the set thickly margined where they meet; females with bc0 cell(s) entire from Mp to R, filled with pigment, remaining blyzocytes usually entire from subtending vein to R, sometimes separated from R by several small irregular cells, dorsally and often laterally margined, bc sets with up to two cells, bc5 with up to four. Rs forked from R approximately one-fourth distance from wing base, with three or four well-defined anterior forks loosely paralleling R; radial+postsectoral areas occupying slightly more than one-third of distal part of wing. Crossvein cu-mp/1r-m moderately robust. Mp_2 forked from Mp near to Rs origin, joining Mp_2+Cua_1 before or after Cua fork; Mp_2+Cua_1 paralleling Mp_1 to wing margin, but becoming somewhat irregular and crooked and sometimes difficult to distinguish from crossveins distad of inflection point. Cua forked proximal to Rs origin in males, somewhat distad of it in females; cubital area occupying slightly more than one-fourth of posterior half of wing. Cubital triangle prefork domain with nine to twelve crossveins, distal domain with one to three crossveins; marginal cell often present, sometimes divided, sometimes broadly joined to triangle, sometimes only connected by Cua_2+Cup. Anal area cells broadening distally. 1A forked approximately one-third distance from wing base to Cua fork, anterior branch fused with Cup, posterior branch fused with posterior wing margin. HW. Similar to FW except as follows. Apical area with nine to sixteen somewhat irregular crossveins. Mp_2 usually forked well after Rs origin, Mp_{2a} sometimes paralleling Mp_1 to wing margin, moderately well-defined and not fused with Mp_1, at other times becoming irregular distad of inflection point, branching and/or otherwise difficult to distinguish; posterior medial area occupying one-fourth of posterior half of wing. Medial triangle long and extremely narrow; prefork domain with 11-16 very short regular crossveins; distal domain without regular crossveins; marginal cell usually present. Anal area with a single triangular cell near wing base. Cup striking a short and somewhat weakly developed 1A, Cup+1A adjoining posterior wing margin well before narrowest portion of wing, sometimes fused with it, separating as wing begins to widen again. 2A more weakly expressed than 3A, 2A continuing no further after 2A-3A fusion but anterior branch faintly visible. *Setae*. Costa basal setae golden brown; subsequent short stiff black setae arranged in four somewhat irregular rows in basal third of wing, these becoming regular and more dense in middle third of wing, then very dense and somewhat irregular again in distal third; posterior axillary setae brown. Nearly all veins, veinlets and crossveins of dorsal and ventral surfaces with short stiff curved black setae. Numerous somewhat short, slender curved dark brown setae on membranes as follows: nearly entire ventral surface of wing, but denser in distal half and on membranes forming blotches, and dorsal membranes in distal portions of costal area, apical area, presectoral area including blyzocytes, pigmented portions of radial area, distal blyzocytes of radial area, and unpigmented extreme distal portion of radial area near apical area. *Color and patterning*. Veins. Costa and Sc yellow to pale reddish, R reddish brown, FW Cua and HW Mp_2 reddish brown, most remaining veins, veinlets and crossveins pale yellowish to dark reddish brown. Membranes. In males, costal area nearly completely filled with pigment, FW and sometimes HW often with pigment lacking in mesal portion of cells; in females, subcostal veinlets thickly margined with reddish brown pigment; apical area blotch with pigment variable, FW: absent in a long narrow submarginal stripe, also a few to several mesal cells margined, halfway filled, or devoid of pigment, HW: absent in a short, narrow, distal stripe near wing apex, also a few to several mesal cells margined, halfway filled, or devoid of pigment; pigment more-or-less completely filling cells in anterior blotch, portions of distal cells of radial area along Sc+R, basal portion of mediocubital area (HW: anterior medial area), cubital triangle (HW: medial triangle), cubital area (HW: posterior medial area) near fork and along Cua_2 (HW: Mp_{2p}), and anal area, including anal process; proximo-mesal cells of anal area thinly margined or devoid of pigment, disto-mesal cells more thickly margined. Male: Entire area of hyaline portions of both wings smoky reddish brown. FW mesal blotch somewhat variable in shape, symmetrically triangular, broadly contiguous with subapical blotch; FW subapical blotch a somewhat even band, mesally swelling very slightly, less than half as tall as mesal blotch, broadly connected to apical blotch; HW blotches Similar to FW. Female: Hyaline membranes mostly lacking any color, some specimens very slightly tinted. FW mesal blotch somewhat variable from a symmetrical to a curved triangle, height slightly less than width at base, sometimes very thinly, other times more broadly joined with subapical blotch; FW subapical blotch variable, swelling somewhat mesally and narrowing slightly before joining apical blotch broadly, one-third to one-half as tall as mesal blotch; HW blotches Similar to FW.

Abdomen. Tergum. T1 plates dorsally dark brown, laterally paler yellow to brownish gray with a dark brown spot at base of each seta, membrane and mesal margins of plates yellow, membrane with less tissue than in other species. T2 acrotergite membrane sagittally yellow, otherwise, with sclerotized portions, dark brown. T2 posterolateral macula short, crescent-shaped, posterior margin of macula and tergite margined with pale yellowish brown. T3 dorsally and anterolaterally orange to reddish brown, posterolateral macula diffuse and uneven, somewhat elongate bell-shaped, darkening dorsodistally. T4 anterolaterally and antero- and posterodorsally orangish to grayish brown, posterolateral macula as on T3, large, a dark brown spot at base of each seta. T5–T8 patterning as in T4, but with posterolateral macula becoming progressively more irregular. T9 laterally dark brown, dorsally pale orangish brown, ventral margin orangish. *Sternum*. S1 brown. S2 brown. S3 brown, often a moderately large sublateral diffuse yellow macula with diffuse dark brown margins near posterior margin, this sometimes darkening to evenly brown, each seta with a diffuse dark brown spot at its base. S4–S7 color as in S3; posterolateral macula visible on S4 and sometimes S5, orangish, subsequent sternites sometimes with very small and diffuse yellowish regions on posterior margins.

Male terminalia (A2 Figs. 100, 101). *Unmacerated specimens.* Ectoprocts dorsally produced, bulbous, proximally yellowish to reddish, posteriorly dark brown. S9 dark brown, internally dark brown. Pulvini often emerging past S9 margin, orangish to dark brown. Gonarcus visible, dark reddish brown dosally and laterally, apically yellow. *Macerated specimens.* Pulvini more proximate to S9 than in other species, length half that of gonarcus, twice width. Setae long, stiff, brown, co-equal in length on ectoprocts and pulvini. GPC, lateral view: length medium, basally only somewhat broad, dorsal and ventral margins subparallel, dorsal surface very weakly arched, more so subapically, slightly darkened, pigment fading to absent at apex, dorsal margin not notched, parameres brown, apex slightly more blunt; ventral view: narrower than long, base slightly narrowed, lateral margins convex, becoming straighter and converging toward apex in distal half, apex acute, wrinkled portion of each paramere approximately one-half width of entire paramere, darkened, orangish; inter-parameral groove slightly broader in apical portion, pelta pale yellowish, inconspicuous.

Female terminalia (A2 Figs. 32, 34, 102, 103). *Unmacerated specimens.* Ectoprocts dorsally produced, bulbous and reddish to brown, mesobasally paler. Ventrovalvae yellowish to reddish brown; linguella and distivalvae reddish brown. *Macerated specimens.* Distivalvae small, height approximately two-fifths that of ectoprocts, round, well separated from one another, very proximate to ectoprocts. Ventrovalvae only slightly elongate, proximate to distivalvae, somewhat broad, apices slightly produced distad but not ventrad in lateral view. Linguella small, membranous but somewhat robust, paired transverse lobes very proximate to one another, appearing largely fused, bearing short stiff dark brown setae. Interdental space shape triangular or shield-shaped; interdens sclerotized base shape a somewhat large diamond, sclerotized dark, sagittal blade length short, in profile only moderately high, irregularly curved to somewhat quadrate.

Variation. Female bc1 completely filled with pigment (JRJ_01259). Hyaline tint somewhat fainter in males JRJ_01033 and JRJ_01260. Specimen JRJ_01238, a female, with hyaline membranes considerably tinted, but still much less than males; this is the only female in all of *Tmesibasis* specimens examined in which the membranes are conspicuously tinted, if only slightly. Yellow maculae at posterior margins of S3–S7 not visible in most specimens. Pulvini not extending outside of keel in all undissected specimens.

Primary type.—

Tmesibasis waelbroecki van der Weele, 1909. Holotype ♀, IRSNB, not examined. *Type locality*: Democratic Republic of the Congo, Kinshasa, Kinshasa [-4.331652°, 15.313920°], 284 m. *Label data*: “Kinchassa, Waelbroeck May 16 1899”. *Condition*: unknown. *Notes*: Although the holotype was not examined for this study, *waelbroecki* is an unmistakable species, and the conspecificity of the additional material examined is not in question.

Additional material examined.—*Central African Republic*: [MHN: 1 ♀, JRJ_01238 (A2 Figs. 10, 13)]. *Côte d'Ivoire*: Vallee du Bandama [CIRAD: 2 ♂♂, JRJ_01035 (A2 Fig. 98), JRJ_01036 (A2 Figs. 22, 96); USNM: 1 ♀, JRJ_01038 (A2 Figs. 32, 34, 97, 102)]. *Democratic Republic of the Congo*: Bas Congo [RMCA: 1 ♂, JRJ_01165, 1 ♀, JRJ_01173]; Orientale [RMCA: 1 ♀, JRJ_01166]. *Gabon*: Haut-Ogooue [MNHN: 1 ♀, JRJ_01236]. *Ghana*: Ashanti [UMMZ: 1 ♂, JRJ_01033]; Brong Ahafo [UMMZ: 1 ♂, JRJ_01034]; Northern [CAS: 1 ♂, JRJ_01032 (A2 Fig. 19)]. *Kenya*: Nandi [BMNH: 1 ♂, JRJ_01260]. *Nigeria*: Abia [BMNH: 1 ♀, JRJ_01259 (A2 Fig. 5)]; Anambra [BMNH: 1 ♂, JRJ_01258 (A2 Fig. 11c)]; Bauchi [BMNH: 1 ♂, JRJ_01250 (A2 Figs. 7, 100, 101)]. *Togo*: Plateaux [CIRAD: 1 ♀, JRJ_01037 (A2 Fig. 8)]. *Uganda*: Rubirizi [USNM: 1 ♀, JRJ_01007 (A2 Fig. 103)].

Natural history.—Several adult specimens were collected at light sources, including one explicitly at a black light trap. Two specimens collected on November 23 and 24, 1982, were taken at lights at 8 PM and 7:30 PM, respectively.

Discussion.—In a genus full of species with remarkable appearances, *T. waelbroecki* stands apart as one of the most charismatic. This is attributable to its broad, highly falcate wings (especially the hind wings) with acute apical angles, its well-developed and broadly contiguous wing blotches, and the very dark color of the wings of males. Before this study the male was undescribed (van der Weele 1909: 93).

As recorded here, *T. waelbroecki* has the broadest distribution of any *Tmesibasis* species, having been recorded from as far west as Cote d'Ivoire and as far east as Kenya, thus spanning the African tropical belt. This distribution seems to indicate a close association with tropical climates, perhaps more so than in other species.

Final thoughts and future research

Tmesibasis species, though rather large and dramatically colored and patterned, have been under-collected, and even with this revision, most remain very poorly known. The treatments of most species are based on very few specimens, and virtually nothing is known about their life histories.

The genus appears to comprise primarily tropical species, but at least one, *T. larseni*, is found in rather arid regions along the southern and western coastlines of the Arabian Peninsula, where it is endemic. A geographic 'hotspot' of *Tmesibasis* diversity appears to be the Uganda-Kenya-Tanzania region, in which half of the species can be found. Countries/regions for which few or no records are known, but which might also host populations, especially if we allow for consideration of more arid climates, include Angola, eastern Namibia, Botswana, Mozambique, Zambia, Democratic Republic of the Congo, Ethiopia, South Sudan, Central African Republic, Congo, Cameroon, and southern Chad. It is likely that additional new species remain to be discovered.

Males of all species are known, and females are known for all species except *T. simplex* and *T. scopsi*, which should be a high priority for future collecting. Contemporaneously captured male and female series are needed to further confirm or refute the hypotheses of male-female conspecificity proposed here. Additional collecting is also needed to corroborate species concepts and fill out distribution ranges.

The dramatic patterns found on the wings, thorax and abdomen of *Tmesibasis* invite questions about their practical value to the species; an initial hypothesis is that the coloration functions as protective camouflage. Further collecting and field observation are necessary to determine what habitats *Tmesibasis* occupy, what constitutes normal flight and roosting behaviors, what role their striking physical appearance plays in adult biology, and what morphological, habitat, and ecological characteristics are of the immature stages. The collection of gravid females in order to rear and describe larvae will be an important first step in beginning to determine the life history of this beautiful group of lacewings.

CHAPTER IV

TAXONOMIC REVISION OF THE ENTIRE-EYED OWLFLIES (NEUROPTERA: ASCALAPHIDAE: HAPLOGLENIINAE) OF THE WESTERN HEMISPHERE

Synopsis

A cladistic analysis of 79 morphological characters of all body regions is used to taxonomically revise the entire-eyed owlflies (Haplogleniinae) of the Western Hemisphere. In the analysis, only one of six traditional genera, *Amoea* Lefèbvre, is recovered as monophyletic, and is placed as one of two large clades. *Ascalobyas* Penny is placed into two separate but adjacent small lineages at the base of the second large clade. The remaining ingroup species are placed into the second large clade. Within this second large clade, *Haploglenius* Burmeister is broadly paraphyletic with respect to the remaining traditional genera: it contains a monophyletic *Neohaploglenius* Penny, *Verticillecerus* van der Weele and *Ascaloptynx* Banks, each at the end of a pectinate stem. In order to recognize monophyletic groups, a new classification is proposed, which comprises four genera: *Amoea*, the new small genus *Neascalobyas*, a reduced *Ascalobyas*, and a broadly redefined *Haploglenius*, which contains five new species groups, three of which represent the former traditional genera. In addition, new species in every genus and nearly every species group are described, many existing names are recognized as synonyms, and previously described species herein recognized as valid are redescribed. In the four genera, a total of thirty-seven valid species (thirteen new) are

here recognized. All species are figured, and maps of their distributions are provided. *Episperches molinai* Navás and the fossil species *Amoea electrodominicana* Engel and Grimaldi are removed from *Amoea* and are placed within *Ameropterus* Esben-Petersen and Haplogleniinae *incertae sedis*, respectively. *Ascaloptynx oligocenica* Nel is also removed from the novel *appendiculatus* species group (formerly *Ascaloptynx*) within *Haploglenius* and placed within Haplogleniinae *incertae sedis*.

Introduction

The family Ascalaphidae Lefèbvre, 1842, commonly called owlflies, is a moderately small family of lacewings (ca. 450 described extant species) divided into three subfamilies. Of these, the subfamily Haplogleniinae Newman is the second largest, with ca. 95 described extant and two fossil species, and comprises those species that have an undivided eye and antennae extending past the origin of Rs in the forewing in spread specimens (in the other two subfamilies the eyes are divided by a transverse depression [Ascalaphinae], or the antennae do not extend past the origin of Rs [Albardiinae]). Haplogleniinae are nearly cosmopolitan, being absent only in Australia and Europe. In the Western Hemisphere, the subfamily contains 24 valid extant and two fossil species in six genera and two tribes (Penny 1982a, Oswald 2013a).

The cohesiveness of the Haplogleniinae of the Western Hemisphere, or New World Haplogleniinae (NWH), has rarely been called into question. Exceptions include van der

Weele's (1909) and Tjeder's (1992) suggestion that *Ascaloptynx* Banks might belong with the African genus *Melambrotus* McLachlan. Within the NWH, however, there have been questions as to the monophyly of the tribes and genera (Ardila and Jones 2012), and species (Penny 2002). Penny (1982a), in his generic review of the NWH, diagnosed Verticillecerini Orfila, 1949 as having a prominent axillary (anal) angle at the base of the forewing, and Haplogleniini Newman, 1853 as not having the anal angle prominent. Within Haplogleniini, he diagnosed *Haploglenius* Burmeister (1839) as having 2A present and long in the hind wing. Ardila and Jones (2012) explained that Penny's 2A is actually a series of aligned crossveins, and revised the diagnosis to be the presence of three well-developed rows of anal cells in the hind wing anal area. A new species recently described by Ardila and Jones (2012), however, has both three rows of anal cells in the hind wing, and the forewing axillary angle well-developed. Thus the new species (*Haploglenius abdominevittatus* Ardila & Jones) does not fit cleanly within *Haploglenius*, nor into Verticillecerini. Regarding the nine valid species of the genus *Amoea* known at the time, Penny (2002) argued that they differed only in size and intensity of a single color pattern, and suggested that they might all constitute a single species.

Taxonomic history

The taxonomic history of the NWH is long and, for at least a handful of its species, rather complicated. Early descriptions were simple, based on a single or small series of poorly-labeled specimens, and mostly lacked high quality illustrations. Profound challenges were presented to subsequent authors who often did not have access to the original type material and had little material of their own. As a result, their treatments of species were fraught with misidentifications and disagreements about synonymies. However, the combination of historical information with type material made available for this study has allowed for a correction of misidentifications and a resolution of taxonomic inconsistencies. A summary of the literature, including some of the most important complications, is provided here. More detailed coverage is provided in the taxonomic treatments of each taxon presented later in this work.

Olivier (1790) described the first entire-eyed owlfly from the Western Hemisphere, the clear-winged *immaculatus* from South America, which he placed in Fabricius's genus *Ascalaphus*. In 1793, Fabricius (1793), described *Ascalaphus appendiculatus* from an unknown location (first inferred to be North America by Rambur [1842]). Nearly fifty years then passed until Burmeister (1839) described two new species of *Ascalaphus* from Brazil (*A. costatus* and *A. subcostatus*). He further described characters (e.g., entire eyes, slender body) and provided a name, *Haploglenius,* for a genus to contain those two species, in effect erecting the genus (in spite of his comments that he was leaving the decision to create such a genus to future authors). In characterizing *Haploglenius* (= 'simple-eyed') he was the first to separate out divided-eyed owlflies from entire-eyed ones. Subsequently and almost simultaneously, Lefèbvre and then Rambur (both 1842) published competing treatments of the world's owlflies. Lefèbvre's work, which was meant to serve as an introduction to a much larger (but ultimately never published) monographic revision, included a key to the 'Ascalaphides' based on his classification in progress. It included several new genera of entire- and split-eyed owlflies (but not *Haploglenius*) and characters to define them. In at least two cases, however, characters for his genera (*Ptynx* and *Orphne*) did not match the attributes of the species he included within them (*costatus* Burmeister and *appendiculatus* Fabricius, respectively). Rambur's work also presented keys and new genera (and included *Haploglenius*) and separated the owlflies into split-eyed and entire-eyed forms (as did Lefèbvre), an approach followed by nearly all subsequent authors in their keys and classifications. Though complete, it introduced additional confusion by incorrectly synonymizing Burmeister's *costatus* and *subcostatus* with Fabricius's *appendiculatus*, by suggesting that *Haploglenius* males have the wing bases appendiculate and females have them entire, and by describing the new genus and species *Byas microcerus* from an obscure and anomalous specimen ambiguously originating from "Antilles".

Subsequent authors did not immediately follow Rambur or Lefèbvre's generic naming conventions. Walker (1853) acknowledged Rambur and Lefèbvre's divisions and names, and incorporated their ideas about classification into his, but chose to list all previous genera and species of owlflies under *Ascalaphus* Fabricius when he evaluated specimens in the collection of the British Museum. His work treated all the New World species known at the time and included descriptions of eight new species; most of those are confirmed here as junior synonyms of previously described species or one another.

Hagen (1861), in his synopsis of the Neuroptera of North America, reviewed all taxon names of owlflies of both North and South America but again included all species under *Ascalaphus*. He suggested Rambur's *microcerus* to be *costatus* Burmeister, thereby treating it as a separate species to Walker's (1853) *albistigma*. He also placed the entire-eyed *chlorops* into his "eyes sulcated" group. In 1866, Hagen published his synopsis of the "Hemerobidarum", where he provided a revised synonymy of the owlflies, placing 15 NWH species group names under eight valid species mostly into Rambur's genera: *Byas* (to contain the ambiguous *microcerus*), *Suhpalacsa* Lefèbvre (for *chlorops* and numerous split-eyed species), and *Haploglenius* (all the other NWH species). He placed Lefèbvre's genera *Amoea*, *Orphne* and *Ptynx* as synonyms of *Haploglenius*. This synonymy provided increased order to the entire-eyed owlflies by treating nearly all the known names within the owlflies and by clearly separating out the growing number of known New World species from the Old World ones. Limitations to Hagen's work, however, include the mis-association of at least a dozen species-group names, despite his ability to view many specimens. Brauer (1868) provided the first identification key that included *Haploglenius* and *Byas*.

McLachlan (1871) presented the first monograph of the Ascalaphidae. In addition to presenting a review of the literature predating his work and summarizing all known biology for owlflies, he described their morphology in detail and presented a new classification and generic key. His work recognized three valid genera of NWH, and he described three new species. During the latter parts of the 19th century, many new NWH species were described, by Blanchard (Blanchard and Brullé 1845), Walker (1860), McLachlan (1891), and Gerstaecker (1885, 1894). Gerstaecker (1894) also described *Episperches*. Van der Weele (1906) reported on his examinations of numerous type specimens and proposed many synonymies. He followed up shortly after with his comprehensive monograph “Ascalaphiden” (1909). In the monograph he recognized six genera of American “Holophthalmine, including one new (*Verticillecerus*), described three new species, and presented black and white photographs of nearly all the species, including types. His work addressed all of the taxonomic problems encountered prior and discussed numerous questions arising from insufficient representative material. Nevertheless, though detailed, his taxonomic treatments do not completely resolve some of the more problematic taxa, including *Amoea* and *Episperches*, *chlorops*, *microcerus* and *albistigma*, and *appendiculatus* and *juvenilis*. Also, his keys are unwieldy (the couplets are long paragraphs), complicating identifications. New species descriptions were abundant in the following years, with new names being added primarily by Navás (1909, 1911, 1912, 1914, 1920, 1923a, 1923b, 1927, 1929, 1930, 1931). Other authors sought to improve higher level nomenclature: new generic replacement names were proposed by McClendon (1906: *Neuroptynx*) and Banks (1915: *Ascaloptynx*), and new tribe and subfamily names for NHW taxa were authored by Navás (1912b: Episperchini, Neuroptyngini), Handlirsch (1936: Neuroptynginae), Orfila (1949: Verticillecerinae, Verticillecerini), Stange (1967: Episperchinae), and MacLeod (1971: Ascaloptynginae). Williner (1945) included a few high quality black and white photographs of NWH in his overview of species from Argentina.

Shetlar (1977) revised the Nearctic Ascalaphidae in his doctoral dissertation. In this revision he made many changes to the existing classification, including synonymizing numerous taxa under a few concepts. His taxon limits for at least some of the genera and species appear to have been too inclusive (e.g., *Haploglenius*, *Amoea immaculata*), though, based on examinations of type specimens conducted in this study. But he also provided important solutions for other problematic taxa, for example synonymizing *Episperches* under *Amoea*, and *albistigma* under *microcerus*. Shetlar also presented excellent coverage of the literature and provided detailed illustrations of internal and external anatomy of larvae and adults. However, his work was never published beyond his dissertation and only some of his synonomies have been adopted. Penny (1978) provided a comprehensive list of Amazonian taxa, including synonyms. Shortly after (1982a) he reviewed and revised the generic classification of the New World Ascalaphidae, presenting the new replacement name *Ascalobyas*, describing the new genus *Neohaploglenius*, and synonymizing *Episperches* under *Amoea*. In his corresponding treatment of the Ascalaphidae of the Amazon basin (1982b), he described two new NWH species and created numerous synonymies based on examinations of type specimens. He also presented identification keys and illustrations for all included taxa. These two papers helped to stabilize the taxonomy and nomenclature of the NWH, which had become bloated and disorganized in the post-van der Weele period. But some of his revisions presented new concerns. For example, he adopted Orfila's (1949) tribal concepts for the NWH, grouping together all genera with narrow wing bases (a derived feature) into Verticillecerini, and those with convex bases (a plesiomorphic feature) into

Haplogleniini, thus creating likely paraphyletic groups and had not been tested phylogenetically.

In recent years, several papers have been published that have added new information and stability, as well as new questions. Oswald and Penny (1991) reviewed the genus group names of all Neuropterida, correcting many nomenclatural errors, including assignments of type specimens and validity of names. Penny et al. (1997) adopted Shetlar in synonymizing all three species of *Ascalaptynx* under *appendiculatus* in their catalog of Neuropterida occurring north of Mexico. Penny (2002) treated the NWH of Costa Rica and synonymized two species of *Neohaploglenius*. He also suggested all nominal species of *Amoea* probably represent just a single species. New fossil species of putative NWH were described by Nel (1991) and Grimaldi and Engel (Engel and Grimaldi 2007). Ardila and Jones (2012) described a new species of *Haploglenius* from Colombia and suggested changes to the genus diagnosis. And Ábrahám reviewed the genus *Haploglenius*, describing one new species and creating new synonymies.

This work presents a species-level cladistic analysis of the NWH, based on 79 morphological characters of all body regions, in order to test the monophyly of its tribes, genera and species. The results of this analysis are used to present a new classification. In addition, taxonomic revisionary work, which occupies the bulk of this paper, treats all known species and provides new identification keys, descriptions, illustrations, and distribution maps, as well as other information.

Materials and methods

Material

Approximately 1200 specimens were made available for this project by the following research collections (see A3 Excel File 1). Codens are taken from Arnett et al. (1993) where available. This list also includes collections from which specimens were not borrowed but which are referenced in this work. These are marked with an asterisk (*).

AMNH*	American Museum of Natural History, New York, New York, USA
BHMH*	Museu de Historia Natural, Universidade Federal de Minas Gerais, Minas Gerais, Belo Horizonte, Brazil
BMNH	The Museum of Natural History (British Museum of Natural History), London, UK
BYUC	Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA
CAS	California Academy of Sciences, San Francisco, California, USA
CLEV	Cleveland Museum of Natural History, Cleveland, Ohio, USA
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
CUAC	Clemson University Arthropod Collection, Clemson University, Clemson, South Carolina, USA
DEBU	University of Guelph Insect Collection, Guelph, Ontario, Canada

EMAU *	Ernst-Moritz-Arndt-Universität Greifswald, Greifswald, Germany
EMEC	Essig Museum of Entomology, University of California, Berkeley, California, USA
EMUS	Utah State University Entomological Museum, Utah State University, Logan, Utah, USA
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA
INPA	Colecão de Invertebrados, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil
JRJC	Joshua R. Jones personal collection
MACN*	Museo Argentina de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina
MCLPC*	R. McLachlan private collection
MCZ*	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MFNB	Museum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany
MHN-ICN*	National Institute of Natural Sciences, Universidad Nacional de Colombia, Bogotá D. C.
MHNG	Muséum d'histoire naturelle, Geneva, Switzerland
MNCN*	Museo Nacional de Ciencias Naturales, Madrid, Spain

MNHN	Muséum national d'Histoire naturelle, Paris, France
MSUC	Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan, USA
MZPW*	Museum of the Institute of Zoology, Polish Academy of Science, Warsaw, Poland
NAVC*	R. P. Longinos Navás private collection
NMW	Naturhistorisches Museum Wien, Wien, Austria
OXUM*	University Museum of Natural History, Oxford, United Kingdom
RMNH*	Naturalis Biodiversity Centre, Leiden, Netherlands
SCMK*	Somogy County Museum, Kaposvár, Hungary
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
SDMC	San Diego Natural History Museum, San Diego, California, USA
SELYS*	SELYS (Michel Edmond de SELYS-LONGCHAMPS [1813-1900], private collection)
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA
TAMUIC	Texas A&M University Insect Collection, Texas A&M University, College Station, Texas, USA
UCDC	R. M. Bohart Museum of Entomology, University of California, Davis, Davis, California, USA

UMMZ	Museum of Zoology – Insect Division, University of Michigan, Ann Arbor, Michigan, USA
UMRM	Enns Entomology Museum, University of Missouri, Columbia, Missouri, USA
UMSP	University of Minnesota Insect Collection, University of Minnesota, St. Paul, Minnesota, USA
UNAB	Museo Entomológico Universidad Nacional Agronomía Bogotá, Universidad Nacional de Colombia, Bogotá, Colombia
UNESP	Universidade Estadual Paulista, Jaboticabal, Sao Paolo, Brazil
USNM	Smithsonian National Museum of Natural History, Washington, D.C., USA
WSU	Maurice T. James Entomological Collection, Washington State University, Pullman, Washington, USA
ZMH*	Martin-Luther-Universität, Zoological Museum, Halle-Wittenberg, Sachsen-Anhalt, Germany
ZMUH*	Universität von Hamburg, Zoologisches Institut und Zoologisches Museum, Hamburg, Germany
ZSM*	Zoologische Staatssammlung, Munich, Germany

Specimen examination, preparation, dissections, photography, and illustrations

Both pinned and dissected specimens were visualized under a Leica MZ6 dissecting microscope enabling magnifications from 6.3 to 40 times. Specimens were prepared following the protocols detailed in chapter 1. See chapter 1 for a detailed explanation of the methods used to capture photographs and create illustrations.

Terminology

Anatomical terminology is extracted from a number of sources, including Adams (1958), Aspöck et al. (1980), Penny (1982a), New (1984), Tjeder (1992), and the Torre-Bueno Glossary of Entomology (Nichols 1989). In the course of this study it was also necessary to create some new descriptors specifically for the Haplogleniinae of the Western Hemisphere, or "New World Haplogleniinae". These terms are listed and explained under 'Adult morphology', below.

Abbreviations and annotations

In addition to terms introduced in chapters 1 and 2, this chapter uses the following abbreviations: ASG, *appendiculatus* species group; ESP, *extensus* species group; FSG, *flavicornis* species group; GSG, *gerstaeckeri* species group; m, meters above sea level; MV, mercury vapor light bulb; NWH, New World Haplogleniinae; P1, P2, etc., pleural membrane of abdominal segment 1, 2, etc.; UV, ultraviolet light source; RSG, *reticulatus* species group.

Etymology and nomenclature

Etymologies were determined using Brown (1954) and various web-based resources, including Oswald (2013a) and Wiktionary (http://en.wiktionary.org).

Novel nomenclatural acts in this paper are in **bold text.**

Databasing

All specimens examined in this work have been assigned and had attached to their pin or placed in their cryogenic tube a JRJ (Joshua R. Jones project) database number. See chapter 1 for a complete explanation of the database, its purpose and the protocols followed for its implementation. The portion of the database dedicated to this project is presented in A3 Excel File 1.

Adult morphology

This section follows the format of that of previous chapters. It is meant to augment the formal descriptions provided later in this work by presenting and defining new terms created in this study (marked with an asterisk*), discussing anatomical features of the NWH that are unique among owlflies, and expanding upon aspects of anatomy beyond what is presented within the formal descriptions or the results of the cladistic analysis. All anatomical terms used in this work are underlined in this section.

Head

Specialization. The genera that comprise the NWH have simple head morphologies. They exhibit no ornamentation or other conspicuous derived features beyond what might be characterized as the 'typical' owlfly ground plan. The paraocular band is less than half the width of the frons and glabrous, the extra-torular sclerites are narrow, the prefrons is small, hardly larger than the footprints of the toruli, and the pleurostoma is absent. The palpi are unproduced and setosity of mouthparts is consistent with that in non-NWH species.

Eyes. Shape is often slightly oblong dorsoventrally, and in many species a very subtle, almost imperceptible, mesal flattening occurs. This flattening often corresponds with a very slight enlargement of either the dorsal or ventral portion of the eye. In a few taxa (*Ascalobyas*, *Neascalobyas*) the mesal flattening is greater, but not quite furrow-like. Some species of *Haploglenius* have the eye nearly spherical and no mesal flattening is seen.

Plates. In *Allocormodes*, the mesal part of the vertex bears two distinct, undivided, colorful (yellow to dark red), glabrous sagittal plates, an elongate anterior one on the high point of the crown that bifurcates into short arms posteriorly, and a short ovoid one just posterad of it on the back of the head. In addition, subtriangular lateral plates with similar color and texture encroach mesad onto the vertex from the orbital sclerites. In NWH, these same plates are seen but they are significantly reduced and have unique shapes, colors and textures. The anterior sagittal plate is reduced to an often inconspicuous (they are often concolorous with the vertex) pair of very narrow parasagittal bands, also posteriorly bifurcate, but with a matte or granular texture. The posterior sagittal plate is ovoid to narrowly cordate (often posteriorly acuminate and striking, or nearly striking, the margin of the foramen), and distinctly divided by the cranial suture into two halves, and has a similar color and texture to the anterior plates. The lateral plates are usually very inconspicuous but can be seen in a few species. They have irregular shapes; the largest plate, positioned dorsally, often is claw- or donut-shaped, and their color and texture matches that of the sagittal plates. This suite of plates is found in all species, but they are often so subtly expressed as to be nearly imperceptible, and they are also often obscured by dorsal setae. For these reasons are not included in species descriptions.

Thorax

Cervical sclerite. This structure is fairly consistent in shape and size across the NWH, with some slight differences in the dorsal texture in a few species. The sclerite is slightly less robust than that seen in other haplogleniine genera such as *Allocormodes*.

Pronotal valve*. The valve refers to the posterior flange of the pronotum, which in males of several genera and species is produced posterad over the mesonotal acrotergite and mesoprescutum. The flange may be somewhat produced (with length slightly variable) but unarticulated, or it may be very produced and laterally articulated. In the most derived condition it is quite large and overlaps the acrotergite and mesoprescutum completely, and has distal dorsal wrinkles that enable it to curve or drape the sclerites beneath with a shallow cupping shape. Although not yet confirmed in every taxon (due to inadequate numbers of museum specimens for some species and difficulty in observing the inner surface of the valve when it is closed), in species with the valve articulated (and possibly only in those species), the ventral surface of the valve is coated with a brilliantly white, crystalline, possibly waxy, substance. This substance, when present, forms a rather thick layer. It is likely chemically similar in makeup, if not identical, to the thin dusting of pruinescence seen on the pleural stripes of conspecifics and other related species.

The valve was considered taxonomically relevant by some authors (e.g., McLachlan 1871, van der Weele 1909, etc.), and its biological purpose has been discussed by several others (Tjeder 1992: 36 provides a nice review). Most recently, it was evaluated by Onore et al. (2014), who were able to observe in the field live specimens of *Haploglenius neoguineensis* Navás from Ecuador (identified as *Haploglenius latoreticulatus* van der Weele). In their daytime observations they witnessed cryptic males who had secreted themselves amongst tree roots rhythmically opening and closing the valve, creating a blinking signal, whenever the observer's shadow passed over them. They indicated this flashing of the "bright white spot" was akin to the signalling of fireflies, and suggested the valve performs a function in courtship. Such an idea was initially put forward by Eisner and Adams (1975) on the basis that the structure only occurs in males. Eisner and Adams (1975) also observed a captured specimen of *Haploglenius* in the field, which responded to being prodded and seized by flexing the valve to expose the white patch. They first proposed that the valve filled a defensive function by startling would-be predators. A third purpose for the valve was proposed by Penny (1982b: 619), who suggested it might be involved in the release of sex pheromones. While all three hypotheses provide reasonable explanations and all may be actual purposes of the valve, the fact that the inner surface bears a highly reflective inner coating (and is not only membranous and flexible), and that this has now been confirmed to perform a signaling function in undisturbed males, suggests that communication may be the primary function of the adaption.

Mesonotal acrotergite. In most NWH species this sclerite has a smooth dark grayish surface and a simple, unproduced posterior margin. In males with the pronotal valve well-developed, the ventral surface of the valve is contiguous with the acrotergite, and together these surfaces are semi-membranous and flexible and bear a very dense pile of very short fine pale setae which is often coated with the crystalline white substance mentioned above. In a small handful of *Haploglenius* species, the distal margin of the acrotergite is distinctly bilobed and diagnostic.

Pleural patterns and setae. Patterning of the thoracic pleuron is highly diagnostic for several genera and species of NWH. In *Amoea*, some species have the pleural sclerites highly variegated, that is, portions of individual sclerites bear one color while other aspects of the same sclerite have another, and the overall appearance of the pleuron is highly irregular and patchy; the colors are shades of brown and yellow. In other species the color has become organized into a lateral band of yellow that runs from the anterior to the posterior reach of the pteropleuron immediately ventrad of the wing bases; this band is termed the subalar stripe*; the rest of the pleuron is variegated to varying degrees. In at least one other species the area ventrad of the subalar stripe is further organized into a brown subtending pleural stripe*. In *Ascalobyas microcerus* (Rambur) the subalar stripe is weakly expressed. In *Ascalobyas oswaldi* n. sp. and *Neascalobyas*, the pleura are evenly brown without maculation. In *Haploglenius*, nearly all species bear a pair of pale to intense yellow oblique stripes* that extend ventrad from the posterior region of each wing base to the anterior face of the subtending leg coxa; these stripes are secondarily lost in a few species. Setae on the pleuron are somewhat variable but typically not very dense, and more or less consistent in length and density; a few exceptions occur and are often diagnostic, and these are noted in the species descriptions. Color of the pilosity varies from white to yellow to brown.

Legs

Specialization. Legs in NWH are rather short as in other haplogleniines. No specializations or derivations are observed. Coloration is rather similar amongst the genera but is vitally important for identification of one species of *Neascalobyas*.

The tarsi vary in color among species, and in at least one species group (*gerstaeckeri*) are distinctly yellow or very pale red. Very commonly, though, the tarsi are medium to very dark reddish brown, nearly black, and in these species the apical margin of the terminal tarsomere is reddish, orangish, or pale brown. This feature helps to unite all NWH (see 'Cladistic analysis').

Tibial spurs. The spurs are very weakly curved, straighter than in non-NWH owlflies. They are short, slender and almost straight in some *Amoea*, more robust slightly more curved, but not longer, in *Ascalobyas*, slightly more robust and curved and extending almost to distal margin of third tarsomere in *Haploglenius procerus* n. sp., and slightly longer in other *Haploglenius* spp.

Wings

Wing shape. The basiposterior wing margins of many NWH species, more than in most genera of Haplogleniinae from other parts of the world (notable exceptions include *Allocormodes* and *Protidricerus*—see 'Morphology' section in chapter 1), have a rather plesiomorphic, that is convex, shape. Broad wing bases with convex forewing and hind wing margins occur in *Amoea*, *Ascalobyas*, *Neascalobyas*, and a few species of *Haploglenius*. This broadened area is referred to in this work as the pre-Mp_1 area* (= hind margin of anal and medial areas). Narrowing of the wing bases is a repeated trend within *Haploglenius*. The evolution of this wing feature is discussed in detail in the 'Cladistic analysis', below.

Pterostigmata. The pterostigmata are rather simple in most NWH but occur in a few rather unique conditions for some species and species groups. The *extensus* species group, for example, is diagnosed by the distal margin of the yellow pigment of the pterostigmata, which has a very elongate crescent shape. In the *appendiculatus* species group, the pterostigmata veins are inclined and the pigment highly reduced. In a few other species of *Haploglenius*, the pterostigma veins and membranes are dark. Specifics are provided in the formal genus, species and species group descriptions, and in the cladistic analysis.

Subcostal area pseudoveinlets*. When examined very closely, all NWH have the subcostal area membrane surface gently undulating as it passes the base of each subcostal veinlet in the costal area. In a handful of *Haploglenius* species, these undulations are marked with brown pigment; when elongate the pigment resembles margined veinlets. Some species (or individuals within species, or the hind wing [HW] of individuals, versus their forewing [FW]) merely have a spot at each undulation where the Sc membrane joins Sc, but do not have the pigment produced into a line.

Deltus*. In the FW is a basal cell contained by R, 1r-m, and Mp. This name of this cell is a Latinized form of the Greek *delta*, given in reference to the cell's distinctly triangular shape. The pigmentation of this cell is, in some species groups, diagnostic. The cell completely lacks pigment in the *appendiculatus* group, for example, as well as in a few species of *Amoea*. It is distinctly colored in others. In most *Haploglenius* species the cell is translucent brown, with the anteromesal portion along R thickening and becoming opaque. In some *Amoea* species, the opaque portion occurs on one side of cell or the other.

Curve of Mp_2 + Cua_1 and Mp_1. Navás (1920), in his description of new species *Haploglenius eurypterus* Navás, interpreted the sharp curve of terminal region of the cubital veins (=Mp_2 + Cua_1 and Mp_1) to be diagnostically important. This feature was examined and described in all species descriptions in order to evaluate this hypothesis. In fact, in several *Haploglenius* species the veins curve sharply before striking the hind margin of the wing. As the degree of curvature is varies continuously and is a bit difficult to characterize in some species, it was not coded in the cladistic analysis.

Patterning and color. Wing patterning in NWH, while commonly subdued or subtle, is nevertheless often diagnostic at all taxonomic levels. *Amoea* mostly lack wing maculation (with a few exceptions—some species have the subcostal and costal areas weakly infuscate, and at least one species has some males distinctly melanistic). Several species in *Neascalobyas*, *Ascalobyas*, and *Haploglenius* have broadly darkened wing apices. *Ascalobyas* and most *Haploglenius* have dark costal areas. Some *Haploglenius* species have subcostal pseudoveinlets (see above), and several have a long stripe formed by the infuscation of the cells subtending R. Two species of *Haploglenius* have dramatic reticulate margining of the cells subtending R. In addition to the species of *Amoea* with some males strongly melanistic, several species in *Ascalobyas*, *Neascalobyas* and *Haploglenius* also display weak melanism, including occasionally in females.

Abdomen

Length and breadth. Relative (to wing length) abdomen lengths across the NWH genera are fairly consistent, varying slightly among genera from approximately two-thirds to slightly less than the full length of the wings when they are folded over the back; in *Amoea* and the *appendiculatus* species group, for example, male abdomens approach the wingtips in length, but in most *Haploglenius* the abdomens are shorter. Generally, lengths are slightly shorter in females than in males. As in many other owlfly lineages, males generally have more slender abdomens and females have stouter ones, but feeding increases mass considerably in both sexes (and cannot necessarily be used as the only diagnostic tool for sexing specimens). Egg development in females also leads to great distensions of the pleural membrane. A single species of *Haploglenius* in the *appendiculatus* species group has the abdomen of males extending beyond the wings when they are folded over the back.

<u>Tergal process</u>*. In males of one species in the *appendiculatus* species group, the distal margin of T3 is produced into a erect, narrow, thinly fluted, more-or-less-elongate, often apically bifurcate process. In its sister species the distal margin of T3 sometimes bears a single or pair of very tiny nubs.

<u>Pleuritocavae</u>. These are eversible pouches or finger-like protrusions of the pleural membrane of males at the distal margin of abdominal segments 7 and 8. They occur in some of the more derived species of *Haploglenius* and show considerable variation in length and breadth (with the anterior pair always larger than the posterior pair), usually between species but sometimes within them. In the most dramatic examples, the organs corkscrew greater than one full turn and are covered in numerous deep wrinkles, the dorsal surface is very dark, and the ventral surface is brilliantly white to yellow. These structures have been noted by several authors (van der Weele 1909: 48, Penny 1982b: 619, Tjeder 1992: 30); Tjeder (1992) considered them to be homologous to similar

structures occurring in other genera of Neuroptera, including *Nevrorthus*. The purpose for these structures is unknown, but their membranous and eversible nature suggests a role in the emission of pheromones. Their conspicuous coloration in several species also suggests a part in courtship displays and mate attraction by visual means.

<u>Hooding</u>*. Males in the *angulatus* and *extensus* species groups exhibit conspicuous shape and color patterning on abdominal segments 7 and 8. Expressed somewhat differently from species to species, the basic morphology is thus: the posterior margin of T7 is flared slightly to considerably above the dorsal surface of T8 (“hooding”), exposing it and the underside of T7; the same occurs to a lesser degree at the distal margin of T8, exposing the dorsal surface of T9; these exposed surfaces are often brilliantly colored pale white to yellow, with some variation in the expression of a distal dark maculation, and the dorsal surfaces have a reduced density of setae; S7 and S8 flatten out, rather than curving dorsad, forcing the pleural membrane laterad; pleuritocavae often exert from underneath the distal fold of this membrane where it overlaps the subsequent segment.

In specimens that are macerating but not yet fully cleared, the source of the brilliant coloration becomes evident: the sclerite surface in the area of the pale color is very transparent, more so than other surfaces, and the inside surface of the sclerite is coated in a dense layer of pale fat bodies.

Patterning. The tergites of many species are more or less evenly brown and lack patterning. In *Amoea*, a handful of species express faint parasagittal stripes, and these are often imbedded with small dark diffuse spots. In *Haploglenius abdominevittatus* Ardila & Jones, a portion of each tergite bears very fine reflective setae that, from a distance, is visualized as a broad pale transverse stripe. In the *appendiculatus* species group, the antecostal scars are often distinctly pale; in two species diffuse dark maculations anterad and posterad of the scars appear, these becoming developed into triangles in *Haploglenius juvenilis* (McLachlan, 1871). In the latter two species, the sternites are distinctly marked with parallel longitudinal black and white or yellow stripes. In most other NWH, the sternum is brownish, and often very diffusely pigmented with varying degrees of yellowish coloration.

Terminalia

Ectoprocts. These are entire and undeveloped in all males and females of NWH, as in most genera of Haplogleniinae.

Genitalic variation. Unlike in *Allocormodes* and *Tmesibasis*, two African genera of Haplogleniinae, there is little to no species-level variation in most of the genital structures of each of the genera treated in this study, and most closely-related species are indistinguishable from one another based on the genitalia alone. Across the NWH, males have the GPC entire and simple, with the pelta simple and parameres not projecting, and females have mostly unremarkable valvae, and the interdens a simple short pin. There are some real differences that transition across the genera (but do not necessarily break at the genus level), however, for example in the shape of the dorsum of the GPC, in the length and expression of the pulvini and their setae, and in the shape of the ventrovalvae, but even these are somewhat subtle. One remarkable exception occurs in the *appendiculatus* species group; here, males have elongate pulvini, and the parameres are produced and tusk-like, and in the females the interdens is completely lost. But these features are common to all three species and their slight variations cannot very effectively differentiate between them.

Preimaginal and specialized adult morphology, general biology, and ecology

Descriptions of preimaginal semaphoronts and their external morphology (i.e., eggs, larval instars, pupae, exuviae) are presented in New (1971) and Henry (1972, 1976, 1977, 1978a, 1978b). Adult female internal ovarial morphology is presented in New (1971). Morphology of the adult male pleuritocavae is discussed in Tjeder (1992). Morphology, field observations, and further discussion of the adult male “startling patch” (= pronotal valve) are presented in Eisner and Adams (1976), Tjeder (1992), and Onore et al. (2014).

Investigations and discussions of ecological and biological phenomena, including life histories and various larval and adult behaviors, are addressed in Henry (1977, 1978a, 1978b) and Tjeder (1992).

NWH taxa whose biology has been explored are *Ascalobyas* Penny, 1982a [as *Byas* Rambur, 1842: New (1971), Henry (1978a)], *A. microcerus* [as *Byas albistigma* (Walker, 1853): Henry (1978b)], *H. juvenilis* [as *Ascaloptynx furciger* (McLachlan, 1891): Henry (1972, 1976, 1977, 1978a, 1978b)], *Amoea* Lefèbvre, 1842 [as *Episperches* Gerstaecker, 1894: Henry (1978a)], *Amoea arenosa* (Walker, 1853) [as *Episperches arenosus* (Walker, 1853): New (1971)], *Haploglenius brunneus* n. sp. [as *Haploglenius luteus* (Walker, 1853): Eisner and Adams (1976)], *Haploglenius costatus* (Burmeister, 1839) [Tjeder 1992], *H. luteus* [Tjeder 1992], and *H. neoguineensis* [as *Haploglenius latoreticulatus* van der Weele, 1909: Onore et al. (2014)]. Details regarding these individual taxa are covered in more detail in their respective taxonomic treatments presented later in this work, under the header "Preimaginal and specialized adult morphology, general biology and ecology".

Cladistic analysis

Overview

Most authors have not questioned the monophyly of the NWH and have treated it as a cohesive entity (McLachlan 1871, Navás 1912b, Orfila 1949, Shetlar 1977, Penny 1982a). Van der Weele (1909: 56), however, postulated that *Neuroptynx* (treated here as the *appendiculatus* species group, or ASG) is more ancient than other NWH and has little relationship to them, and instead is more closely related to the African haplogleniine genus *Melambrotus* McLachlan, asserting the two genera 'sprung from a common stock'. He based his assertion on common wing form, body setosity and 'whole habit'. Tjeder (1992: 40) also briefly entertained this idea, pointing out that in both genera the wing membranes are "partly haired" and the pulvini long and projecting. Henry (1978a) explored the evolution of several larval and adult characters in the phylogeny of owlflies and hypothesized a monophyletic NWH based partially on the presence of repagula, a trait unique to the NWH and Ululodini, an ascalaphine tribe. As additional evidence for a close relationship between the ASG (as *Ascaloptynx*) and *Ascalobyas* (as *Byas*—Henry1978b) he gave 'absence of dorsal littering, 180 degree jaw 'ambush' position with its associated head and jaw morphology, retention of two sets of body scoli, dorsal placement of first and second abdominal spiracles, and modification of setae into scales [=dolichasters]'. Tjeder (1992: 52) observed in the few Afrotropical larvae known, they show different coverings of dolichasters than those seen in

Ascaloptynx and *Ascalobyas*, and, seemingly contradicting his earlier position that the ASG is more closely related to *Melambrotus*, suggested that "such differences will prove to be of taxonomic importance."

Monophyly of the tribes and genera within the NHW was discussed by Ardila and Jones (2012), who described a new species of *Haploglenius* that expressed features of both *Neohaploglenius* Penny and *Haploglenius* Burmeister. The species *abdominevittatus* expresses the following features of *Neohaploglenius*: the anal angle produced and triangular, the wings moderately narrow, and verticils not well developed; of *Haploglenius*: the HW 2A long. Ardila and Jones placed *abdominevittatus* in *Haploglenius* because they interpreted the presence of the 2A (which they explained is not 2A but an aligned series of crossveins) to be more conserved than wing narrowing. They explained that the existence of a species of *Haploglenius* expressing features of *Neohaploglenius* calls into question the monophyly of the tribe Verticillecerini Orfila, which has as its diagnosis "forewing with prominent axillary angle at base of anal margin". Verticillecerini currently contains the genera *Neohaploglenius*, the ASG (as *Ascaloptynx*), and *Verticillecerus* van der Weele. *Haploglenius* is currently included in the tribe Haplogleniini with *Ascalobyas* Penny and *Amoea* Lefèbvre. The latter tribe is diagnosed as having the "forewing without prominent axillary angle at base of anal margin". As discussed in chapter 1, wing narrowing is a frequent phenomenon observed across the Ascalaphidae, and even occurs within genera. Thus the current taxonomic basis of the tribes and genera within the NWH may not correspond with their evolutionary history, and they may not be monophyletic. Ardila and Jones called for a revision of *Haploglenius* and of all Neotropical haplogleniine species.

A clear need has existed to test the monophyly of the NWH, its tribes and genera. This section presents a cladistic analysis of the species of NHW based on morphological characters.

Character selection and data analysis

Intensive species-level revisionary work was performed, resulting in a determination of 36 species within the NWH. All were initially included in the analysis, but one, *Haploglenius legnotos* n. sp., is known only from a single female. It lacked enough characters to provide a confident placement and was removed (see further discussion below). A 37th species, *H. brunneus*, was discovered after completion of the cladistic analysis, and was not included. It is very similar to *H. luteus* and is interpreted to be sister species to it.

Extensive pinned material was made available for this study and many species were well-represented. Some, however, appear to have been more rarely collected, and for these only a few specimens were available. Specimens were examined thoroughly and evaluated for conserved and informative characters. Attention was paid to structures determined to be useful in previous studies (see chapters 1 and 2), as well as to new features that appear to be unique to or derived within the NWH species and genera. Care was made to eliminate characters that are inconsistent within species, ambiguous in their expression, or continuous and difficult to quantify.

Characters were included from all major anatomical systems typically recognized and treated in Neuropterida. Seventy nine characters of the head, thorax, wings, legs, and abdomen were ultimately included and utilized. These are provided in list format below (See ‘Characters’).

The greatest number of features discovered and scored are in the wings, but antennae, thorax, abdomen and genitalic characters are also well represented. A large number are sex-specific, with the majority (27) coming from males. Most characters are binary, but several are multistate. Character scorings can be seen in A3 Table 1.

Computational methods

Analysis was performed in TNT (Tree Analysis Using New Technology: Goloboff et al. 2008). Searches were run using the ‘New Technology’ approach, with the Sectorial search, Ratchet, Tree-drift and Tree-fusing algorithms all employed under default settings. No characters were designated as additive, although the putative plesiomorphic state was coded as 0 and derived states as 1, 2, etc. Bremer supports were generated using the Bremer supports function, retaining trees suboptimal by 20 steps. The analysis was rerun in PAUP* (Phylogenetic Analysis Using Parsimony *And Other Methods: Swofford 2002). Bremer supports were calculated in PAUP* using TreeRot (Sorenson 1999). The consistency index (C. I.) retention index (R. I.), and other statistical measures were generated in PAUP*, as were lists of taxon synapomorphies by branch (A3 Table 2) and character changes by character (A3 Table 3).

Outgroup taxa

Genera of NWH exhibit common wing shapes and venation, color patterns of the wings and thorax, chaetotaxy, and genital morphology, and thus generally have been regarded as monophyletic, but no synapomorphies have previously been proposed to unite them. Because the Haplogleniinae are presumed to be more closely related to one another than to Ascalaphinae, and the NWH constitute all Haplogleniinae in the Americas, a haplogleniine outgroup was sought from outside of the Western Hemisphere.

Few workers have addressed higher-level phylogeny for Haplogleniinae or Ascalaphidae that might provide clues in outgroup selection. Winterton et al. (2010) presented a comprehensive phylogenetic analysis of the Neuropterida, but included only two Ascalaphidae, and no Haplogleniinae. Henry (1978b) presented a simple phylogeny for the Ascalaphidae focused on New World genera. His phylogeny suggested a close relationship between the NWH and the New World ascalaphine tribe Ululodini, based on three characters (ovarioles, repagula, eyes). It also suggested a mesal position for the NWH within the Ascalaphidae and did not resolve other tribes in the family.

Haplogleniinae from other parts of the world inferred to be primitive based on their expression of plesiomorphic traits (e.g., un-narrowed wing bases—see chapters 1, 2, 4) were selected as outgroups. These include *Allocormodes nigristigma* Jones, an African species, and *Protidricerus elwesii* (McLachlan), a species from east Asia. *Albardia furcata* van der Weele, the sole representative of the owlfly subfamily Albardiinae, is inferred to be the most plesiomorphic extant taxon within the family on the basis of its very short antennae. It was also included. Recent unpublished molecular evidence (chapter 4) has confirmed that *Melambrotus* does not group closely with the ASG (*Ascaloptynx*) as van der Weele (1909) and Tjeder (1992) hypothesized, but instead belongs in a monophyletic clade with other African Haplogleniiinae, and it was not included.

Ingroup taxa

The analysis resulted in the recognition of several species groups, to be discussed under 'Results' below. For ease in discussing characters, the abbreviations for those species groups (ASG, ESG, FSG, GSG, RSG—see 'Abbreviations and annotations' above) are used.

Characters

The following character systems, characters and states were used in this analysis. See A3 Table 1 for coded matrix.

Size

[1] FW length, males

0 >35 mm

1 <35 mm

Pre-analysis comments: Within the ingroup there seems to be a bimodality in size, with the various genera being notable for having either generally smaller or generally larger species. *Amoea*, for example, are generally smaller, with one exception, as are the GSG; *Haploglenius*, on the other hand, are typically larger. The threshold value for male wing length (as a proxy for species size) selected for this character falls within what appears to be a gap in size difference for the majority of species examined. A small number of species includes members with dimensions near the threshold value selected; a few of these even include individuals that are larger and smaller than the cutoff. These species were coded for both states.

Head

[2] Vertex anterior mesal plate and parasagittal area

0 plate at least moderately well-developed: slightly raised, breadth variable, glossy; parasagittal area variable in breadth, depressed

1 plate rather poorly developed and sometimes difficult to see: not raised, narrow and posteriorly bifurcate, glabrous with a granular texture; parasagittal area broad, not depressed

Pre-analysis comments: A raised and yellow colored mesal plate (state 0) is particularly well-expressed in the outgroup *Allocormodes*. Evidence of a vestigial plate of similar shape and position (state 1) but with distinct differences (as characterized above) can be seen in all species of the ingroup.

[3] Vertex lateral plates

0 undifferentiated and appearing as a single undivided plate

1 differentiated, shiny, distinctly colored, well-separated by conspicuous depressed innervations of parasagittal area

2 differentiated, but appearing more as a textured area than a plate, texture shiny and granular in appearance, often indistinctly colored, area sometimes small or narrow, parasagittal innervations often difficult to see

Pre-analysis comments: These plates vary amongst the outgroups. Within the ingroups the expression of these 'plates' also varies considerably, but with consistent patterns as characterized in the parameters above.

[4] Frons and vertex setae density and color, males

0 very sparse to somewhat dense, color variable, but if denser then not dark brown to black

1 very dense from frons to vertex, dark brown to black

Pre-analysis comments: *Ascalobyas nigrantia* males have a thick shock of setae from frons to vertex (state 1) that easily separates them from their sister species *A. machadoi*. *Protidricerus* has similar dark frontal setae.

[5] Clypeus color

0 variable, black, evenly dark, or orangish brown, but dorsolateral macula not apparent

1 evenly yellow, with no dark maculae on dorsolateral corners

2 color variable, pale yellow to amber, with dorsolateral corners bearing a dark reddish brown maculation, but this very diffuse and indistinct, dull, or very small (macula incipient or vestigial)

3 bright yellow, with dorsolateral corners bearing a large dark reddish brown stripe or macula, this sometimes diffuse but distinct

Pre-analysis comments: The presence of incipient dorsolateral clypeus maculae (state 2) is a common feature within the ingroup. In a few species of *Haploglenius*, however, the maculae are well-expressed (state 3).

[6] Labrum color

0 black

1 dark brown, sometimes only in distal half

2 pale yellow to amber brown

3 reddish amber

Pre-analysis comments: In *Haploglenius handlirschi* and a few other *Haploglenius* species the labrum is distinctly dark brown (state 1). In the GSG it has a particularly reddish cast (state 3).

[7] Antennae length

0 not extending past FW Rs origin

1 extending past Rs origin but not past FW Rs 2nd fork

2 extending past FW Rs 2nd fork

Pre-analysis comments: Most ingroup species have the antennae considerably long (state 2), but in *Ascalobyas*, the ASG, and *Haploglenius procerus* the antennae do not reach past the second fork of Rs in the forewing in spread specimens (state 1).

[8] Antennae verticils

0 absent

1 present on mesal surface of nodes of first three or four flagellomeres, a few to several, often aggregated, approximately coequal in length with a single flagellomere

2 present on mesal and occasionally also lateral surface of nodes continuing past the fourth flagellomere, often to sixth, seventh or further, a few per flagellomeres, unbunched or in groups of two or three, at least several with length varying from that of one to three flagellomeres

3 present on mesal and lateral surfaces of all nodes nearly to club, and often completely ringing nodes, those on basal nodes longer than three flagellomeres and shortening on successive nodes, continuing far down flagellum

Pre-analysis comments: Penny [1982a] relied on the presence on the antennae of "whorls of long setae" to diagnose and name *Verticillecerus*, but several ingroup species in other genera also express verticils, notably *Haploglenius costatus*, *H. normani*, the ASG, *H. abdominevittatus*, and *H. extensus*, although their expression varies (states 1, 2, 3) somewhat amongst these taxa.

[9] Antennal internodal setae

0 absent or very sparse

1 present, numerous

Post-analysis comments: State 1 was only observed in the ASG.

[10] Antennae type and color patterning

0 flagellum normal, nodes and internodes more or less concolorous

1 flagellum normal, nodes distinctly pale

2 flagellum normal, nodes dark, node apex thinly very pale whitish, base of each flagellomere pale yellowish

3 flagellum robust, nodes concolorous or thinly pale

4 flagellum robust, nodes more broadly pale

5 flagellum normal, nodes dark, node apex thinly very pale whitish, apex of each flagellomere pale yellowish

Pre-analysis comments: In *Amoea* the nodes and internodes are essentially concolorous (state 0), but paler nodes seem to occur in most other ingroup taxa.

[11] Antennal club type

0 capitate, apex very round and spherical (symmetrical) in silhouette

1 cylindrical, elongate and apex blunted

2 pyriform, apex very slightly blunted (symmetrical)

3 fusiform, rather long and somewhat narrow, with apex acuminate (often slightly asymmetrical)

4 fusiform, subspherical, apex brief but acuminate

Post-analysis comments: Symmetrical and spherical clubs (state 0) are the plesiomorphic state for the ingroup and occur in *Amoea* and *Ascalobyas*. Fusiform clubs (states 3, 4) are seen in most species of *Haploglenius* and in the GSG. Pyriform clubs (state 2) are seen in the ASG.

Thorax

[12] Pronotum posterior flange, males

0 unproduced posterad, or very short but unarticulated, interior surface lacking white coating

1 produced into an articulated flap or valve, interior surface with white coating

Pre-analysis comments: The shape of the posterior margin of the pronotum posterior flange varies in its expression within the NWH, namely in the size of the valve and its color patterns and textures. As its size seems to vary continuously when well-expressed, it was coded simply as absent/present.

[13] Pronotum posterior flange valve, exterior (dorsal) texture

0 smooth, similar to that of integument on remainder of pronotum, not velvety

1 velvety

Pre-analysis comments: The velvety texture (state 1) occurs distinctly in *Ascalobyas* and *Neascalobyas*, where it corresponds with very dark coloration. A few species in the other genera express it, but usually to a lesser degree.

[14] Pronotum posterior flange color pattern, males

0 evenly medium brown

1 pale yellow to orange with margin dark brown to black and sagittal line often also dark

2 dark brown with numerous yellow marks

3 mesally darkening to very dark brown, otherwise evenly medium brown without other markings

4 evenly dark brown to almost black, with a sagittal diffuse reddish-brown stripe, and margin often narrowly pale brown

5 mesally dark brown to almost black, otherwise reddish or orangish brown

6 broadly and evenly brown to dark brown mesally and pale brown to yellowish to orange sublaterally; sometimes brown again laterally; orangish areas forming anterior portions of pteronotal sublateral stripes

7 evenly honey brown to dark brown, mesodistally slightly darkened, anterolateral area with a diffuse paler brown to yellow macula not reaching to lateral margin

8 orange

9 evenly medium brown with lateral margins thinly yellow

10 (A) reddish brown

11 (B) mesally somewhat dark reddish brown, margins brown, occasionally much paler

Pre-analysis comments: Pronotal color patterns are fairly conserved in *Amoea* and the ASG, but show great variety and are highly diagnostic in species of *Ascalobyas*, *Neascalobyas*, and *Haploglenius*.

[15] Pronotum posterior flange valve marginal wrinkles, males

0 absent

1 present, a few to many

Pre-analysis comments: Wrinkles (state 1) occur in species with the prescutellar valve large, and in several of these species the distal margins of the valve curl ventrad, but not all species that have large curling valves express the wrinkles; in particular wrinkles are lacking in the GSG and ASG.

[16] Mesonotal acrotergite, males

0 unproduced

1 with carinate posterior margins forming a ventral plate on which pronotal valve rests, distinctly emarginate or bilobed

Pre-analysis comments: State 1 is shared by *Haploglenius luteus*, *H. brunneus*, and *H. neoguineensis*.

Post-analysis comments: State 1 is highly derived.

[17] Pronotum and mesoprescutum setae, males

0 somewhat dense, long, pale orangish yellow

1 sparse to dense, more or less medium length, grayish or golden to dark brown

2 somewhat sparse to only intermediately dense, only moderately long, very pale yellow to white

3 somewhat sparse, long, stiff, mostly brown with some medium length wispy gray mixed in

Pre-analysis comments: The ASG and several species of *Amoea* have setae with distinct colors and other attributes as characterized above. Most other species in the analysis have essentially golden brown setae, but these vary somewhat in density, length, and hue, even within species, and thus are difficult to distinguish, and so are placed in a common category.

[18] Cervical sclerite, color

0 entirely brown

1 apex yellow, proximal portion predominantly yellow

2 apex with dorsal portion narrowly yellow, otherwise sclerite surfaces dark brown

3 apex yellow, other surfaces brown

Pre-analysis comments: Very similar color patterns are seen the ASG, FSG, and two species of *Haploglenius*.

[19] Pteronotum maculations

0 absent or consistently dull, indistinct

1 present, at least sometimes distinct on some part of the pteronotum

Pre-analysis comments: Most ingroup species express at least some yellowish maculations on some part of the pteronotum (state 1), most often on the lateral surfaces of the mesoprescutum, but also sometimes on the lateral surfaces of the mesoscutellum and mesally on the posterior swelling of the same, and elsewhere. Several species express distinct longitudinal stripes (char. 17), which can extend from the pronotum to the base of the abdomen. A few taxa appear to have lost most traces of maculations (state 0), namely *Amoea iniqua*, *Ascalobyas*, *Neascalobyas*, and *Haploglenius procerus*.

[20] Pteronotum longitudinal stripes

0 absent

1 present, parasagittal, pale

2 present, sublateral, dark

Pre-analysis comments: Pteronotum longitudinal stripes (state 1) occur in females but not males in at least one species. It was coded as present for that species.

Post-analysis comments: State 1 is diagnostic in the few species that express it and helps to unite sister species in several small species groups.

[21] Pleuron patterning and color

0 color evenly brown or dull orange, or with some slight variation

1 with a distinct, broad, yellow, longitudinal subalar stripe having at least somewhat well-defined ventral margin

2 variegated, but predominantly yellowish with very few brown markings, and no hint of a broad stripe

3 distinctly variegated, with irregular brown and yellow maculations, predominantly darker, with no hint of a pale stripe

4 variegated, but predominantly yellowish with very few brown markings, occasionally with a short broad diffuse yellowish stripe, more mesally situated on pleuron

5 a pale yellow oblique stripe extending from subalar area of each wing anteroventrad to meso- and metathoracic coxal area

6 distinctly variegated, with irregular brown and yellow maculations, neither predominantly yellow nor brown, with no hint of a pale stripe

Pre-analysis comments: Various distinct patterns of variegation (states 1–4, 6) occur in most species of *Amoea* and in *Ascaloptynx*. A distinct broad longitudinal subalar stripe (state 1) characterizes several *Amoea* species. Broad paired oblique stripes (state 5) occur throughout *Haploglenius*, the FSG and the GSG. In the outgroups and *Neascalobyas* patterning is essentially absent (state 0); in *Ascalobyas,* a very weak subalar stripe is expressed, and females and sometimes males show variegation (state 3).

[22] Stripe subtending subalar stripe

0 absent, or present but narrow, irregular, or poorly defined

1 present, broad, well defined, brown

Post-analysis comments: State 1 is an autapomorphy for *Amoea impediens*.

[23] Subalar chaetotaxy

0 undifferentiated from that on remainder of pleuron

1 forming a thick white coat along subalar stripe

2 concentrated into a tuft of moderately dense, long, white setae on meso- and metanepisternum

3 concentrated into a tuft of dense, long, white setae on mesanepimeron

Pre-analysis comments: There is a fair amount of variation amongst members of the ingroup in the density and color of the pleural setae of the thorax, from rather sparse to quite dense, and from white to pale yellow to golden brown. These variations seems to occur to some degree even within species, and were difficult to characterize for the purposes of phylogenetic inference. A few species, however, consistently expressed uniquely distributed setae of distinct density and color patterning; these were characterized as such and coded for (states 1–3).

Post-analysis comments: States 1–3 represent apomorphic conditions.

[24] Thorax pruinescence

0 absent

1 in males only, often present, covering entire pleuron and notum

2 in males and females, present on pleuron only, and evenly so

3 in males and females, present on pleuron only, on oblique stripes

Pre-analysis comments: Not all examined specimens of pruinose species exhibited pruinescence. To prevent ambiguity in the analysis these species were simply coded as ‘present’.

Legs

[25] Coxal setae

0 very dense, very long, yellow on all coxae

1 moderately dense, moderately long, dark brown to black on all coxae

2 dense, moderately long, white on all coxae

3 from rather sparse to moderately dense, somewhat short to moderately long, pale yellow to yellow

4 dense, moderately long, yellow on prothoracic coxae, white on remaining coxae

Pre-analysis comments: In the ingroup, long white setae on all coxae (state 2) occur in *Ascaloptynx* and many closely related species of the FSG and *Haploglenius*. The GSG has a similar condition but with the prothoracic coxae yellow (state 4).

[26] Tarsi coloration

0 completely and evenly black

1 evenly yellowish-red to reddish brown

2 reddish brown to nearly black, but with apical portion of terminal tarsomere distinctly paler, yellow or orange to reddish brown

3 basal 4 tarsomeres reddish brown, terminal tarsomere yellow

4 evenly yellow

Pre-analysis comments: Tarsi coloration is highly variable, even within species. Pale tarsi (state 4) occur in the GSG. Most other NWH have the tarsi reddish to dark brown with the terminal tarsomere apically paler (state 2).

Wings

Shape

[27] FW anal angle

0 undeveloped, posterior margin distad of angle straight to very slightly convex

1 undeveloped to very slightly developed, posterior margin distad of angle at least very slightly concave

2 somewhat well-developed but lateral margins of process still obtuse, posterior margin immediately distad of angle at least slightly concave

3 very well developed and produced, process outline an equilateral triangular, posteror margin immediately distad of angle distinctly concave

4 very well developed and produced, process outline a narrow and slightly elongate triangle, posteror margin immediately distad of angle distinctly concave

5 very well developed and produced, lateral margins of process mesally parallel and slightly curving, apex strongly acuminate

6 somewhat well-developed, proximal margin circular, posterior margin immediately distad of angle at least slightly concave

Pre-analysis comments: Development of the anal process is inferred to have resulted from reduction of the posterior margin of the wing distad of the angle over time, such that it transformed from from convexity to concavity. Broad FW bases have been demonstrated to be plesiomorphic in other genera (e.g., *Allocormodes*; see chapter 1). This character, however, was not coded as ordered.

[28] HW costal area, costa progression

0 not especially narrow, expands basally before narrowing mesally and then becoming more or less parallel to Sc

1 narrow, unexpanded, parallel to Sc entire length

Pre-analysis comments: Several species with narrow FW bases (character 27) also express narrow costal areas (state 1).

[29] HW basiposterior margin (anal + posterior medial + anterior medial areas) shape, males

0 very convex distad of anal angle but not changing angle at Mp_1, wing rather broad and triangular

1 very convex distad of anal angle but not changing angle at Mp_1, wing somewhat narrow and more strap-like

2 very convex distad of anal angle, distinctly expanded, convexity more or less symmetrical and round, margin distinctly changing angle at Mp_1

3 very convex distad of anal angle, distinctly expanded, convexity slightly asymmetrical (slightly flatter distad) and somewhat broader than in other species, margin weakly changing angle at Mp_1

4 convex distad of angle, but less so than in other species, probably secondarily reduced

5 weakly convex, narrowing slightly at Mp_1

6 only slightly produced posterad and narrowed laterally at angle, concave distad of it until Mp_1

7 produced posterad and narrowed laterally at angle (along flexion line), strongly concave distad of it until Mp_1

Post-analysis comments: As with the FW in other owlflies, in the ingroup the HW largely progresses from convex to concave. However, in males of many species of *Amoea* the wing base has experienced an increase in convexity.

[30] HW anterior and posteror margins, males

0 at least slightly convergent from Mp_1 to wing apex

1 essentially parallel from Mp_1 to pterostigma, then very slightly and briefly divergent

Post-analysis comments: Mesal narrowing of the HW unites *Neascalobyas nigrantia* and *N. machadoi*.

[31] HW apex shape

0 subacute to acute, at least slightly asymmetrical

1 symmetrical, rounded

Post-analysis comments: Rounding of the HW apex unites *Neascalobyas nigrantia* and *N. machadoi*.

Veins

[32] Costal area venation

0 cells entire from Sc to C, undivided

1 cells secondarily split by co-linear crossveins near pterostigma

2 cells secondarily split by unaligned oblique crossveins near pterostigma

Post-analysis comments: Evenly divided distal costal cells appear to be an autapomorphy for *Haploglenius luteus*; it was also seen in a few specimens of *H. brunneus* from Ecuador and one of *H. neoguineensis*. Similarly, division of distal cells by oblique crossveins occurs in many but not all individuals of the two species of the ASG that have it.

[33] Radius coloration

0 even from base to apex

1 distinctly banded brown and yellow

Post-analysis comments: banding of R is an autapomorphy for *H. abdominevittatus*.

[34] FW base, anal area cell rows

0 not formed into rows roughly parallel to Cup +1A

1 formed into a single row of cells roughly parallel to CuA

2 at least two to three cells split in distal portions of anal area row

Pre-analysis comments: Number of rows corresponds to wing narrowing, but some species with a single row have it secondarily divided by oblique crossveins (state 2).

[35] HW pre-Cup axillary disk, color

0 opaque, brown

1 opaque, yellow

2 translucent, colorless to pale yellow

3 opaque, brownish red

Pre-analysis comments: The base of the wings in certain clades of the ingroup often expresses a complex pattern of colors. As one of the most extreme examples, in *H.*

handlirschi several sclerites and the basal portions of several longitudinal veins in the posterior parts of the wings are distinctly orangish yellow, whereas all the remaining venation and sclerites are very deep brown. Other closely related species express similar patterns but to a somewhat reduced degree and with a fair amount of variability. Despite this variability, a small focal point of the colored region in the HW is conserved in its color expression; this point centers on the pre-Cup axillary disk, coded here. For specimens with partially translucent disks, if there was at least some brown pigment on it, it was coded as brown. For specimens with more or less equally brown and yellow disks, these were coded as yellow.

[36] HW base, anal area cell rows

0 not formed into rows roughly parallel to CuA

1 formed into two rows roughly parallel to CuA

2 formed into three rows roughly parallel to CuA

3 formed into one row parallel to CuA

Pre-analysis comments: Penny (1982a, 1982b) considered *Haploglenius* diagnosable by the presence of a long 2A bisecting the posterior-most row of cells in the anal area, and gave this as a key character to differentiate it from other New World Haplogleniinae genera. Ardila and Jones (2012) observed that in *Haploglenius* the 2A actually curves early to strike the posterior margin of the wing near the base and that what appears to be 2A is in fact aligned secondary crossveins. They suggested revising the definition of *Haploglenius* to rely upon having three well-developed rows of cells (state 2) in the HW anal area rather than having a long 2A. Penny considered all other New World Haplogleniinae to lack the long 2A. Under the revised morphological concept suggested by Ardila and Jones, these other genera would be interpreted to have either two rows of anal cells parallel to CuA (state 1), with the second undivided by secondary crossveins, or just a single cell row posterad of CuA (state 3). This character was coded under these revised concepts.

A small handful of taxa express an intermediate (and possibly transitionary) state where some to many, but not all, cells in the posterior-most row are split by crossveins; some of these same taxa have specimens with either one row or two. These taxa are coded as multistate.

Cells

[37] FW subcostal area corrugation

0 absent

1 present, a swelling corresponding to each subcostal veinlet of the costal area

Pre-analysis comments: The membrane undulates, its margin rising near the base of each subcostal veinlet along Sc, and falling in between.

Pre-analysis comments: State 1 only occurs in *Allocormodes*.

[38] Deltus

0 partially to completely filled with brown or dark pigment

1 completely devoid of pigment or pigment very faint

2 proximal half covered with black or very dark brown pigment, distal half transparent

Pre-analysis comments: In taxa that have the deltus pigmented, pigment expression is highly variable. Pigment is absent in the ASG and a few *Amoea* spp.

[39] FW cells subtending R, presectoral area, number and width

0 five to seven, all cells more or less coequal to or narrower than their height

1 six to ten, cell widths highly variable and often much narrower than their height

2 eight (rarely nine), all cells more or less coequal to or narrower than their height

3 nine to fourteen (or more), cells more or less coequal to or narrower than their height

4 seven to nine, one or two distal cells with width twice their height

5 approximately six or seven, width of three or four cells approximately twice their height

Post-analysis comments: Almost without exception *Amoea*, *Neascalobyas* and *Ascalobyas* have eight presectoral cells (state 2). Other ingroup species have nine or more (state 3). A reduced number of very wide cells (state 5) is found only in *Haploglenius decorus*. *Haploglenius decoratus* expresses an intermediate state, with one or two cells being very wide (state 4). Outgroups (states 0 and 1) have similar numbers of cells but vary in regularity of shape.

[40] FW cells subtending R, radial area, size

0 normal, similar in size to other cells

1 most greatly enlarged

Post-analysis comments: Enlarged cells occur in *H. decorus* and *H. decoratus*.

[41] FW intercalary cells

0 absent

1 present

Pre-analysis comments: Small irregular cells (state 1) occur between some of the large cells subtending R, but only in *H. decorus*. Occasionally one or two intercalary cells are seen in *H. decoratus.*

[42] FW secondary division of cells subtending R distad of Rs origin and proximad of first Rs fork

0 absent

1 present, ca. two to four cells more or less evenly divided

2 present, many more than four cells irregularly divided

Post-analysis comments: A few evenly divided cells (state 1) are a synapomorphy for the genus *Protidricerus*. Many irregularly divided cells (state 2) is an autapomorphy for *Haploglenius acuminatus*.

[43] Basal cell of HW costal area

0 almost completely devoid of dark color and sclerotization, mostly translucent to clear, sometimes weakly opaque, often devoid of color, sometimes white or very pale brownish or yellowish

1 anterodistally thickened and dark brown in a small focused area, otherwise mostly translucent to clear, sometimes weakly opaque, often devoid of color, sometimes white or very pale brownish or yellowish

2 anterodistally thickened and dark brown over a large area, almost completely covering membrane, otherwise mostly translucent to clear

3 completely sclerotized, black

4 opaque over entire surface, but clear or milky to yellow to pale brown

5 opaque over entire surface, dark reddish brown

[44] HW medial triangle distal domain shape, cell number, males

0 absent

1 very short to moderately elongate, but cells not especially narrow, with one to three cells

2 very elongate and narrow, with three or more cells

Post-analysis comments: A reduced distal domain (state 1) occurs in species with narrowed hind wings: The ASG, FSG, *H. abdominevittatus*, and the GSG. Elongate domains (state 2) occur as autapomorphies for a few species.

Color

[45] FW subcostal area tinting, males

0 absent

1 present, at least a faint tint

Pre-analysis comments: Tinting (state 1) occurs in a few species of *Amoea*, in *Ascalobyas*, and in many species of *Haploglenius*.

[46] FW subcostal area undulations maculation (pseudoveinlets)

0 absent

1 present, a band of pigment on each undulation corresponding with each subcostal veinlet of costal area

Post-analysis comments: A group of species of *Haploglenius* have the subcostal undulations darkened.

[47] HW mesal darkening

0 absent

1 present

Post-analysis comments: Unique to *H. acuminatus*, the HW has a large very diffuse brownish red tinge commencing at wing midpoint and reaching to approximately the pterostigma posterad of the pigment stripe subtending R (state 1).

[48] Entire wing venation margining

0 absent

1 present

Post-analysis comments: State 1 is an autapomorphy for *Amoea latipennis*.

[49] Cells subtending R in presectoral area, pigment

0 absent

1 anterior portions of at least proximal cells suffused with pale brown pigment, sometimes very narrowly, often pigment margining lateral veinlets' anterior portions

2 lateral veins' entire length, but primarily mesal portions, darkly margined

Pre-analysis comments: Presectoral area pigmentation (state 1) occurs in *Ascalobyas* and *Haploglenius*.

[50] Cells subtending R in radial area, pigment

0 absent

1 a few to several cells laterally margined

2 cells completely suffused with pigment, forming a longitudinal stripe

3 cells thickly margined, and intercalary cells, when present, completely filled with pigment

Pre-analysis comments: The longitudinal stripe (state 2) appears in *H. extensus* and *H. legnotos* (latter species not included in analysis). Cells thickly margined (state 3) occurs in *H. decorus* and *H. decoratus*.

Pterostigma

[51] FW pterostigma veinlet distribution, orientation

0 six or more long, curved, closely aggregated veinlets radiating off Sc and Sc+R proximad and distad of Sc-R anastomosis, none perpendicular to it

1 first aggregated veinlet margined or associated with pigment more or less commencing at Sc-R anastomosis and perpendicular (or nearly so) to Sc, last nearly aligned with R

2 first aggregated veinlet margined or associated with pigment more or less commencing at Sc-R anastomosis but distinctly and consistently oblique to Sc, last nearly in line with R

3 first veinlet margined or associated with pigment commencing considerably proximal to Sc-R anastomosis (at a point greater than height of pterostigma)

Post-analysis comments: Pterostigma pigment begins well before the Sc-R anastomosis in *A. nigristigma* and *H. acuminatus*. In the ASG and FSG the proximal-most veinlets of the pterostigma are almost always inclined distad.

[52] Pterostigma pigment distribution

0 only loosely associated with aggregated veins, partially overlapping them proximally and distally

1 more or less completely falling within veinlet aggregation, especially proximally; if distal spillage present, then slight and associated with cream pigment and a crescent distal margin

2 dark pigment distinctly spilling out into apical area distally

Post-analysis comments: Except for a few exceptions, pigment is only loosely associated with aggregated pterostigma veins in the outgroups and always confined within the aggregated veinlets in the ingroups. *Haploglenius acuminatus* and *H. handlirschi*, the two ingroup exceptions, both have pigment spilling out beyond the margins of aggregated veinlets, the former both proximad and distad of the veinlets, the latter distally.

[53] FW pterostigma pigment dimensions

0 height at Sc-R anastamosis and breadth more or less coequal

1 breadth two to three times height

2 ill-formed, breadth about 1.5 times height

3 anterior portion of pigment wrapping along wing margin in apical area, breadth greater than four times height near Sc-R anastamosis

Pre-analysis comments: Breadth in this case refers to the spread of the pigment and not that of the veinlets associated with the pterostigma.

[54] FW pterostigma pigment distal margin shape

0 diffuse, irregular

1 straight

2 weakly crescent shaped, posterior portion along Sc+R and rarely anterior portion along wing margin extended one cell width or so

3 strongly crescent-shaped, anterior portion following wing margin one to four cells widths, posterior portion with a short piece following along Sc+R one or two cell widths

Post-analysis comments: Weak crescent shaped margins occur in a few transition species of *Haploglenius*; distinct crescent occur in the *extensus* species group (ESG).

[55] FW versus HW pterostigma margining

0 neither FW nor HW pterostigma margined, or both margined

1 HW pterostigma margined, but not FW

Post-analysis comments: HW but not FW veinlets are margined in *Ascalobyas*.

Abdomen

[56] Pleural membrane pattern

0 evenly brown

1 at least sometimes with three to four oblique broad yellow stripes

Pre-analysis comments: In taxa that express the pleural stripes, the patterns are generally, but not always, more visible in specimens with distended abdomens. More usually this applies to females, but it also occurs in males of some species (e.g., *neoguineensis*—see for example Onore et al. 2014 figs. 4, 5 [as *latoreticulatus*]).

[57] S3 pattern

0 completely and evenly blackish brown

1 yellow macula present on anterior margin, remainder of sclerite brown with expression of mesal yellow pigment highly variable, from extensive to strongly reduced, and from very diffuse or speckled to rather narrow and distinct or well-defined

2 yellow macula present on anterior margin, remainder of sclerite evenly brown or dark

3 variable, often evenly medium brown, sometimes with obscure diffuse yellow areas

4 sagittal stripe present, distinct, extending from anterior margin of sclerite to posterior submarginal transverse yellow stripe with well-defined margins along entire length, anterior portion broader and laterally acute

5 sagittal stripe present, usually not extending to posterior transverse yellow stripe, margins diffuse, especially posteriorly, anterior portion broad but not laterally acute

6 sagittal stripe present in anterior portion of sclerite, with well-defined margins, posterior portion broadly fusing with and indistinct from lateral brown areas

Post-analysis comments: The sagittal stripe in the ASG is flanked on each side by a sublateral longitudinal yellow stripe. The distinction of the sagittal stripe appears to be the result of an increased development of the yellow stripes.

[58] Sternite dark portions, color

0 brown or reddish brown

1 very dark brown to black

Post-analysis comments: The dark stripes or maculae of *H. juvenilis* and *H. appendiculatus* are nearly pitch black.

Males

[59] Length

0 much shorter than apex of wings folded over tergum, approximately from half to two-thirds length of FW

1 at least two-thirds length of FW to slightly shorter than apex of wings folded over tergum

2 extending beyond apex of wings folded over tergum

Post-analysis comments: Abdomens reach the pterostigma in *Amoea* and the ASG, but become gradually shorter in most *Haploglenius*.

[60] T1 setae

0 dense, long, wispy, orange

1 dense, long, wispy, dark brown

2 dense, long, wispy, pale yellow or white

3 moderately to very dense, long, wispy, golden brown

4 dense, medium leng, stiff, white, directed erectly dorsomesad

5 moderately dense, long stiff slender black mixed with long slender pale gray

6 moderately dense, long, wispy, dark brown mixed with pale yellow or gray mesally

Post-analysis comments: Erect white setae are an autapomorphy for *Amoea nivea*, for which only males are confidently known (one female may belong to the species, but has the thorax obscured by residues), and thus this character was included as a male character. However, for the few species in this analysis of which only females are known, this character was also coded, on the observation that in other closely related species the setae patterns are similar for males and females.

[61] Tergum setae, T2–T9

0 anterior half of each tergite with a dense coat of long wispy yellow setae, posterior half of each tergite bearing a large lateral tuft of medium long stiff black setae

1 anterior half of T2 and T3 with a somewhat dense patch of medium length pale yellow setae, setae on tergites otherwise rather sparse

2 T2 with sparse medium length wispy dark brown setae, T3 with a few short wispy dark brown setae, T4 essentially glabrous, T5–T9 with an intermediately dense coat of short slender black setae

3 T2 with some medium length wispy golden setae, T3–T9 with a moderately sparse coat of very short slender black setae, this becoming denser, stiffer, and very slightly longer on distal tergites

4 T2–T4 with a moderately dense coat of medium short, wispy, golden or brown setae, these becoming shorter and more sparse distad, T5–T9 with a moderately dense coat of very short slender black setae, this becoming denser, stiffer, and very slightly longer on distal tergites

5 T2–T6 with a dense coat of medium short, slender pale yellow or white setae, this becoming progressively sparser and shorter on distal tergites, T7–T9 with a moderately dense coat of short slender stiff black setae

6 T2–T3 with an moderately sparse coat of medium length, slender yellow or golden setae, this becoming progressively sparser and shorter distally, T4–T9 blending from short slender golden setae to short slender stiff black setae

7 T2 and anterior half of T3 with an intermediately dense coat of medium length stiff black setae mixed with some medium long slender pale gray setae, coat with setae becoming short on posterior half of T3 to anterior half of T5, posterior half of T5 to T9 with setae dense, medium short, slender, stiff, black

Pre-analysis comments: This was coded as a male character, as males and females exhibit difference states. Female *Amoea*, for example, have more or less glabrous terga.

[62] Pleural membrane setae

0 P1–P5 or P6 with a sparse coat of long wispy yellow setae, this becoming very sparse to absent on P7–P8

1 P1–P3 with a dense coat of medium length wispy dark brown setae, P4–P8 glabrous

2 P1–P2 with a somewhat dense coat of medium length wispy dark brown and gray setae, P3–P4 mostly glabrous, P5–P8 with a somewhat dense coat of short slender black setae

3 P1–P2 glabrous, sometimes with a very few wispy golden setae, P3–P8 with a very sparse (and hard to see) coat of very short slender black setae, this becoming less sparse to somewhat dense on P6–P8

4 P1–P5 with a moderately dense coat of medium short wispy dark brown setae, this transitioning on P6–P8 to a somewhat dense coat of short slender black setae

5 P1–P6 with a dense coat of medium short wispy medium brown setae, this transitioning on P6–P8 to a somewhat dense coat of short slender black setae

6 P1–P6 with a dense coat of medium short yellow or golden setae, this becoming very sparse to absent on P7–P8

7 P1–P2 with a very sparse coat of short slender black setae, these becoming denser on P3–P8

Post-analysis comments: Very conspicuous and diagnostic pleural setae are found in several species of *Amoea*.

[63] Tergal process

0 absent

1 sometimes present but very short and expressed only as a tiny nub

2 present, elongate, length variable but more or less well-developed, often bifurcate

Pre-analysis comments: The process (state 2) is a feature of *H. juvenilis*.

[64] Segments 7 and 8

0 unexpanded, not broadened, T7 not held tent-like and open over T8, co-planar with T6 and T8, setae variable, S7–S9 not spread nearly flat

1 expanded and broadened, T8 often held tent-like and open over T8 surface of T7 with setae sparse, short, S7–S9 spread nearly flat

Pre-analysis comments: When fully expressed (i.e., in FSG), segments 7 to 9 have a very dramatic appearance. T7 is held tent-like and raised over T8, its ventral surface not in contact with the dorsal surface of T8, exposing them both completely, S8 dorsally has few very short black setae, the dorsal surfaces of T8 and T9 are pigmented cream or yellow and are often pruinose, the pleuritocavae are very long and everted from underneath T8 and are bicolored (anteriorly dark brown, posteriorly yellow) and corkscrew, and S7 to S9 are spread nearly flat. These various features express themselves differentially across related taxa and are coded under several separate characters and states (chars. 64–67, 69, 70).

[65] T7 ventral and T8 dorsal surfaces, pigment

0 undifferentiated from remained of tergum, brown

1 at least some individuals distinctly and completely or nearly completely cream or yellow

Post-analysis comments: Pigmentation occurs primarily in the FSG and ESG, but incipient coloration is seen in some other species of *Haploglenius*.

[66] T8 dorsal surface, pattern

0 at least mostly brown, sometimes with some yellow

1 mostly yellow but with a distal brown macula

2 completely yellow

Post-analysis comments: Four species of *Haploglenius* express the distal spot.

[67] T9 dorsal surface, pigment

0 undifferentiated from remainder of tergum, brown

1 at least some individuals with some part of mesal surface cream or yellow

2 at least some individuals with some parts of lateral marginal surfaces cream or yellow

Pre-analysis comments: Coloration on T9 is often obscured by residues and seems rather variable within species. If any individual specimen of a species had coloration, it was coded as present.

[68] Pulvini protrusion in undissected specimens

0 not protruding beyond margins of genital capsule

1 protruding slightly beyond margins of genital capsule

2 protruding well beyond margins of genital capsule

Post-analysis comments: Pulvini are mostly reduced in NWH, and not visible in unmacerated specimens, but in a few *Haploglenius* species are slightly longer and barely emerge distally; in the ASG they are well developed and elongate, protruding far from the genital capsule.

<u>Macerated specimens</u>

[69] Pleuritocavae, segment 7

0 absent

1 present, poorly developed, only a slight invagination or pouch in pleural membrane to slightly longer than width at base, straight

2 present, length about two times width at base, more or less straight to slightly corkscrewed, but apex not reaching back to base

3 present, length at least three times width at base, corkscrewed, completing at least one complete turn so apex touches base

Pre-analysis comments: These structures are discussed in depth in 'Adult morphology', above.

[70] Pleuritocavae, segment 8

0 absent

1 present, poorly developed, only a slight invagination or pouch in pleural membrane

2 present, well-developed, length one to two times width at base, more or less straight to slightly corkscrewed, apex not reaching to base

3 present, well-developed, length at least three times width at base, more or less straight to slightly corkscrewed, apex not reaching to base

Pre-analysis comments: These structures are discussed in depth in 'Adult morphology', above.

[71] GPC shape, lateral view

0 base a large and irregular mass or bulb of gonosaccal membrane, apex very small, narrow and sclerotized, dorsum of apex smoothly and weakly arched

1 smoothly arched from base to apex

2 dorsum smooth, not especially humped or arched mesally, base in same plane as apex

3 dorsum irregular, base to midpoint of dorsum slightly arched or raised, offset by notch and in a different plane from apex

Pre-analysis comments: In most NWH, the GPC is more or less entire ventrally and weakly arched dorsally, usually with a mesal notch. The exact shape changes subtly across the species and does not necessarily correlate with genus or species group limits. The ASG has a very unique GPC (see 'Discussion' for *appendiculatus* species group).

[72] GPC dorsal subapical notch

0 absent

1 present, visible in lateral view

Pre-analysis comments: The notch, when present (state 1), may be shallow or deep.

[73] Parameres, ventral view

0 long narrow blades basally fused and mesally open, similar to a split tube

1 similar in appearance to cloven hooves, but projecting from GPC as blades, bases not smoothly transitioning into GPC surface

2 similar in appearance to cloven hooves, entire with GPC, bases smoothly transitioning into GPC surface

3 long acuminate tusks curving dorsad

Pre-analysis comments: As with the gonarcus the parameres are more or less similar in most NWH, with only slight differences, but are highly specialized in the ASG.

[74] Pelta

0 a long narrow surface laterally fused with inside surface of parameres and GPC

1 elongate ovoid

2 simple, unproduced, darkly sclerotized, diamond-shaped

3 simple, unproduced, faintly sclerotized, very narrowly spindle-shaped

4 simple, unproduced, faintly sclerotized, broadly almond-shaped

5 simple, unproduced, faintly sclerotized, almond-shaped

6 a slightly produced dorsoventral carina fused laterally with parameres

Pre-analysis comments: The pelta is a minute sclerotized plate imbedded in the apex of the GPC between the parameres in most NHW, but becomes produced into a carina (state 6) in the ASG.

[75] Pulvini

0 a broad locus, undeveloped into a process, bearing numerous short dark robust setae

1 very small and poorly developed, apex with small apical tuft of intermediately long setae

2 well-developed, length ca. two times width at base, nearly entire surface with long setae

3 reduced to a small swelling at base of GPC, apex with small pale-colored setae

4 small and poorly developed, apex with small apical tuft of very long stiff curving setae

5 well-developed, more than four to eight times longer than width at base, bulb-like, bearing long stiff setae

Pre-analysis comments: The exact shape and dimensions and setosity of the pulvini are visualized best in macerated specimens.

Females

[76] Abdominal tergite maculation

0 absent

1 present, distal margin thinly yellow

2 present, parasagittal stripes cinnamon-colored, broad, very weakly expressed, mesal spot usually very weakly-expressed to absent, posterior spot present, large and very diffuse, or absent

3 present, parasagittal stripes cinnamon-colored, broad, well-expressed but diffuse, mesal spot absent, posterior spot present, small and dark

4 present, parasagittal stripes cinnamon-colored, narrow, well-expressed, not diffuse, mesal spot present, small, round or oval, well-defined, black, posterior spot present, small, round or oval, well-defined, black

5 present, distal margin of each tergite darkened

6 present, a more or less well-developed dark triangular macula projecting anterad and posterad from tergal fascia, which is usually colored pale yellow to white

7 present, a diffuse darkness projecting anterad and posterad from antecostal scar, which is usually colored pale yellow to white

8 present, anterior two-fifths of T3, T4, and sometimes T5 with diffuse yellowish markings and golden microsetae, giving tergum a banded appearance

Pre-analysis comments: Tergal patterns are more consistently expressed in females in *Amoea*, thus this character was coded for females for all NWH. The mesal spot, when present, is positioned on the stripe just anterad of the tergite midpoint, and another just anterad of tergite posterior margin.

<u>Macerated specimens</u>

[77] Ventrovalvae shape

0 flat sclerotized plates

1 thickened, folded membrane

2 elongate and narrow, often narrow basally and broadening to apex and paddle-shaped, but sometimes with lateral margins merely parallel sided, mesally plates not touching

3 slightly longer than broad, broadest basally and narrowing to apex, mesally plates often touching

Pre-analysis comments: A few species have the ventrovalvae conspicuously narrow, but in most species the shape is moderate broad, about two to three times as long as wide in ventral view.

[78] Linguella

0 a flat sclerotized plate

1 a large membranous bulb covered in numerous setae

2 a membranous locus bearing several setae, sometimes slightly expanded but not large and bulbous, and not covered in numerous setae

Pre-analysis comments: The linguella is membranous and mostly undeveloped in NWH, as opposed to outgroups such as *Allocormodes*.

[79] Interdens shape

0 absent

1 a dorsoventrally flattened tab

2 a short conical pin

Post-analysis comments: The interdens is essentially conical or nipple-like in NWH. It is absent in the ASG.

Results

Taxonomic placements and support

The TNT/PAUP* analysis resulted in a single most-parsimonious tree with a completely resolved topology (A3 Fig. 1). The tree had the following statistical properties: length 334 steps; number of parsimony-informative characters: 71; consistency index (CI) = 0.6497; homoplasy index (HI) = 0.3503; CI excluding uninformative characters = 0.6389; HI excluding uninformative characters = 0.3611; retention index (RI) = 0.7776; rescaled consistency index (RC) = 0.5052.

The NWH were recovered as monophyletic. Bremer support was high (node 3: 9), indicating that all ingroup taxa fit comfortably within the group, including the ASG. Synapomorphies for the group are presented in the section heading for the NWH under 'Taxonomic treatments', below. A brief discussion of the traditional genera within the NWH in the context of the phylogeny, including the ASG (as *Ascaloptynx*), and a proposal for a new classification, will follow.

Traditional genera

Amoea Lefèbvre

Amoea was recovered as monophyletic but with low support (node 4: 1). It was also placed as sister to remaining NWH. The tree structure showed *A. immaculata* at the base of *Amoea* followed by *A. chlorops* on a pectinate stem. Van der Weele (1909) discussed the similarity of these two taxa (see discussions for these taxa under 'Taxonomic treatments', below). The basal position of *A. immaculata* was expected—it is more similar to other NWH in size and wing shape than any other *Amoea* species. *Amoea iniqua* and *A. nivea* were placed in the middle of the clade as pectinate branches. In fact, they share few synapomorphies with other *Amoea* species and instead seem to express intermediate states in their pleural patterns and thorax/abdomen setae, and so their mesal position was also not unexpected. *Amoea periculosa* was placed with *A. arenosa* and *A. impediens*; the sister-group relationship of the latter two taxa was the most well-supported in the clade (node 10: 3) on the basis of their shared notal stripes, among other features; together these three taxa express a well-developed subalar stripe. In the other three species, which grouped together (node 11), only *A. flavitaenia* has a well-developed subalar stripe; it was placed basad of the other two and nearest to *A. periculosa* + (*A. arenosa* + *A. impediens*). The terminal two taxa, *A. vacua* and *A. latipennis*, are very similar to one another (both have males which are consistently very pruinescent) and occur together in northern Central America and continue up into Mexico, where their distributions diverge to either coast. The basal position of *A. immaculata* and *A. chlorops*, which occur in southeastern Brazil, contrasted with the North American position of the most derived taxa, *A. latipennis* and *A. vacua*, suggests a direction of biogeographic radiation that warrants further examination. *Amoea* is treated here as a valid genus.

Ascalobyas Penny

Penny (1982b) included four species: *dupuyi*, *microcerus*, *albistigma*, and *machadoi*. Revisionary work presented below removes *dupuyi* Navás from *Ascalobyas* and places it as a junior synonym of *A. immaculata*; it also places *albistigma* as a junior synonym of *microcerus*. In the cladistic analysis (Fig. 1), *machadoi* and the new species *nigrantia* were placed together in a small clade as sister group to (*oswaldi* + *microcerus*) + *Haploglenius*. Bremer support for this sister group relationship (node 13) was 2. Bremer support for the relationship (*oswaldi* + *microcerus*) + *Haploglenius* (node 15) was 3. The clades *machadoi* + *nigrantia* and *oswaldi* + *microcerus* were each supported with a Bremer value of 1. The clade *machadoi* + *nigrantia* is supported by the following synapomorphies: HW conspicuously narrowed mesally and broadened around wingtip; and, costal areas devoid of pigment. It is here treated as the new genus *Neascalobyas*. The clade *oswaldi* + *microcerus* is supported by the following synapomorphy: males with HW pterostigma veinlets thickly margined. It is here treated as a redefined *Ascalobyas*.

Neohaploglenius Penny

Penny (2002) synonymized *angulatus* under *flavicornis*, and added the new species *rondonia*. But evidence presented here and uncovered in separate molecular research (unpublished) found *angulatus* and *flavicornis* to be valid species. Ábrahám (2013) examined the type of *rondonia* and discovered it to be conspecific with *Verticillecerus gerstaeckeri*. In the cladistic analysis, *angulatus* and *flavicornis* were placed as sister taxa with moderate support (node 33:3). However, they were placed deep within a larger clade containing species of *Haploglenius* and other NWH genera. *Neohaploglenius* is here treated a junior synonym of *Haploglenius*, and its species are placed in the new *flavicornis* species group, as discussed in '*Proposed revisions to current classification*', below.

Verticillecerus van der Weele

Like *Neohaploglenius*, *Verticillecerus gerstaeckeri* and its new sister species *acuminatus* were recovered as a monophyletic grouping with moderate support (node 23: 3). But, also like *Neohaploglenius*, the genus *Verticillecerus* was placed at the end of a comb deep within a larger clade containing species of *Haploglenius*. This pectination indicates repeated trending toward narrowing of the wing bases and development of the anal angle into a process, features which define the current genera and justify their placement within the tribe Verticillecerini Orfila, along with *Ascaloptynx*. Chapter 1 discussed this trend of wing narrowing within Ascalaphidae. It occurs repeatedly in every tribe and most genera and seems to be a common parallelism, possibly as a result of a tendency among owlflies to respond morphologically over time to opportunities presented by narrow wings, which include increased maneuverability and hovering capacity but come with a tradeoff of reduced overall speed (Wootton and Newman 2008; see also chapter 2, discussion of wing shape in 'Adult morphology'). So, though monophyletic and readily diagnosable, *Verticillecerus* and *Neohaploglenius* (and *Ascaloptynx*) are yet not separated from their parent genus *Haploglenius* in a way that leaves the taxa along the pectinate branches that spawned them monophyletic. Verticillecerus is here treated a junior synonym of *Haploglenius*, and its species are placed in the new *gerstacekeri* species group, as discussed below.

Ascaloptynx Banks

As with the two genera just discussed, *Ascaloptynx* sits at the end of a pectinate stem (node 24) and represents a branch derived from within *Haploglenius*. Unlike the other two genera, however, the ancestral stem is remarkably long (branch length 30+), so much so that it calls into question the unity of *Ascaloptynx* with the NWH. However, *Ascaloptynx* shares numerous synapomorphies with the NWH. These synapomorphies include the distinct (but subtle) expressions of the vertex plates in size, shape and texture, the presence of a sagittal maculation of the frons and the dorsolateral maculations of the clypeus, the presence of the pronotal valve in the new primitive species *elongatus*, and other features. Molecular data (chapter 4) also indicate that *Ascaloptynx* belongs within the NWH. Van der Weele (1909) and Tjeder (1992) were right to question the ancestry of *Ascaloptynx*, but the morphological and molecular data suggest it was spawned by *Haploglenius*, and not from an African lineage such as *Melambrotus*, the competing hypothesis. If it was of recent African origin, it likely would have grouped more closely with *Allocormodes*, which is a close relative of *Melambrotus*, and likely have been placed outside of the NWH. *Ascaloptynx* is here treated a junior synonym of *Haploglenius*, and its species are placed in the new *appendiculatus* species group, as discussed below.

Haploglenius Burmeister

Haploglenius is a well-supported genus (node 17: 5), albeit with some very derived members. Synapomorphies include the paired oblique pleural stripes of the thorax that are often pruinescent, the presectoral area with 9 to 14 cells, the pre-Mp_1 area of the HW not greatly expanded in males, the pulvini very small and poorly developed, and others (see 'Synapomorphies' for the genus). There are repeated trends within the genus toward the development of verticils, the loss of the pronotal valve in males, the loss of the paired oblique stripes of the thoracic pleuron, and, conspicuously, wing narrowing and the correspondent loss of cells rows in the anal areas of both wings and development of the FW anal process from the angle. Many of these derivations are shared in small groups at the ends of pectinate stems, making them diagnosable but obscuring evolutionary relationships.

Proposed revisions to current classification

In light of the cladistics results, changes in classification are here proposed. The NWH are demonstrably monophyletic, with the following revisions and members (see A3 Fig. 1, black triangles numbered 0–9). *Amoea* and part of *Ascalobyas* are each regarded as monophyletic; the other part of *Ascalobyas* is treated as the new small genus *Neascalobyas*. The small genera *Verticillecerus*, *Neohaploglenius*, and *Ascaloptynx* are considered to be derived lineages belonging within *Haploglenius*, and their names are sunk as junior synonyms. In order to maintain the viability of their diagnosis clusters, which are still useful, they are to be treated as new species groups (and not subgenera) within *Haploglenius*, characterized by their traditional diagnoses. This avoids the alternative approach of splitting *Haploglenius* into many small parts, with each species along the pectinate stems being raised to genus level as a monobasic entity; these entities would each require a new diagnosis and description and need to be established as an independent unit, and only a few of these stem species exhibit highly autapomorphic properties (most exhibit autapomorphies but they may be subtle). Further, such an approach would flood the nomenclature with new names, an undesirable prospect to deal with if future analyses call into question any of the results presented here.

The species groups will have the following names, selected for the oldest and most plesiomorphic member of each group; two of these groups are new and do not correspond to a traditional genus: *gerstaeckeri* species group (GSG), the *appendiculatus* species group (ASG), *reticulatus* species group (RSG), *flavicornis* species group (FSG), and *extensus* species group (ESG). A handful of species are unplaced within *Haploglenius*. Synapomorphies recovered in the cladistic analysis are presented for each of these groups (except for the unplaced species) under their section headings within the 'Taxonomic treatments', below.

Taxonomic treatments

Family Ascalaphidae Lefèbvre, 1842

Type genus *Ascalaphus* Fabricius, 1775

Ascalaphidae Newman, 1853

—Newman 1853 r#4530: 199 {as family}; Hagen 1866 r#460: 380 {as family}; McLachlan 1871.09.14 r#353: 219 {as family}; and subsequent authors...

Ascalaphides Lefèbvre, 1842

—Lefèbvre 1842.04.?? r#3666: {as tribe}; Rambur 1842.12.31 r# 5314: {as division}

Ascalafidei Costa, 1855

—Costa 1855.11.03 r#1953 {as family}

Ascalaphina Brauer, 1868

—Brauer 1868 r#1691: 396 {as family—see Taschenberg 1879: 217}; Taschenberg 1879 r#5954: 217 {as family}

Ascalaphiden van der Weele, 1909

—van der Weele 1909.01.05 r#420: 1 {as family}

Etymology and nomenclatural notes.—Ascalaphidae, from *Ascalaphus*: Ascalaphus (Latinized form of Askalaphos, Greek), named for the protagonist Askalaphos in Greek mythology who was cursed and turned into an owl (see Henry 1977: 179).

Diagnosis.—Eyes large, dominating head; antennae usually very long, extending past origin of Rs in spread specimens (except in Albardiinae), clubbed, flagellomeres of club usually as long as or longer than their width; prothorax shortened longitudinally, length much shorter than width in dorsal view; tarsi approximately coequal in length with tibia and femur of same leg; hypostigmal cell absent; Eltringham's organ absent; terminal venation along hind margin with few forks; larvae with variably developed scolus-like processes, tibia fused to tarsus.

Distribution.—Worldwide in temperate and tropical regions.

Discussion.—In the Western Hemisphere, the family Ascalaphidae is represented by all three of its recognized subfamilies, including the focus of the present work, the Haplogleniinae.

Included subfamilies.—Albardiinae van der Weele, Ascalaphinae Lefèbvre, Haplogleniinae Newman.

Key to the subfamilies of Ascalaphidae of the Western Hemisphere

(adult males and females)

1. Antennae short, not reaching past the origin of Rs in the FW in spread or unspread specimens [Brazil] .... **Albardiinae van der Weele**

1'. Antennae longer, reaching past the origin of Rs in the FW (most easily evaluated in spread specimens) 2

2. Eyes entire, not divided into an upper and lower lobe by a deep transverse furrow [U.S. to northern Argentina] .... **Haplogleniinae Newman**

2'. Eyes split, divided into an upper and lower lobe by a deep transverse furrow [U.S. to northern Argentina] .... **Ascalaphinae Lefèbvre**

Subfamily Haplogleniinae Newman, 1853

Type genus *Haploglenius* Burmeister, 1839

Haplogleniidae Newman, 1853

—Newman 1853 r#4530: cxcix {as family}

Haplogleniinae Newman, 1853

—Tjeder & Waterston 1977 r#6063: 87 {as subfamily}; Tjeder 1980 r#309: 401 {as subfamily}; Penny 1982a r#5105: 392 {as subfamily}; Penny 1982b r#5103: 607 {as subfamily}; Tjeder 1992 r#7246: 59 {as subfamily}

Olophthalmi Lefèbvre, 1842

—Lefèbvre 1842.04.?? r#3666: 6 {as tribe};

—Hagen 1866 r#460: 374, 454 {L, JSYN (of Ascalaphidae sensu Newman)}

Holophthalmi McLachlan, 1871

—McLachlan 1871.09.14 r#353: 230 {as division}

Holophthalminae Weele, 1909

—van der Weele 1909.01.05 r#420: 26 {as subfamily}

Holoftalmos Navás, 1912, part

—Navás 1912b.10.31 r#542: 205 {as section}

—Navás 1913 r#1207: 44 {as section}

Episperchini Navás, 1912

—Navás 1912b.10.31 r#542: 206 {as tribe}

Episperquinos Navás, 1912

—Navás 1912b.10.31 r#542: 206 {as tribe}

Neuroptyngini Schroeder, 1925 {as tribe}

Neuroptynginae Handlirsch, 1936

—Handlirsch 1936 r#2821 {as subfamily}

—Adams 1958 r#1286: 98 {Ph.D. dissertation, nomenclatural acts invalid: as subfamily}

—Henry 1972 r#2875: 1 {as subfamily}

—Henry 1977 r#2877: 179 {as subfamily}

—Henry 1979: r#2879: 273 {as subfamily}

—Aspöck, Aspöck & Hö1zel 1980 r#6747: 312 {as subfamily}

Verticillecerinae Orfila, 1949

—Orfila 1949 r#5020: 188 {as subfamily}

Episperchinae Stange, 1967

—Stange 1967: r#5811: 62 {as subfamily}

Ascaloptynginae MacLeod, 1971

—MacLeod 1971.01.29 r#3958: 155 {as subfamily}

Etymology and nomenclatural notes.—Haplogleniinae, for *Haploglenius* (see etymology for *Haploglenius*, below).

Diagnosis.—Eyes entire, sometimes bearing a mesal or posteromesal flattening or weak depression, but depression not deep or sulcus-like; antennae extending beyond the origin of Rs in spread specimens.

Proposed synapomorphies of Western Hemisphere Haplogleniinae.—vertex anterosagittal plate present but reduced to inconspicuous narrow paired parasagittal bands; vertex lateral plates present but reduced, inconspicuous; clypeus dorsolaterally with vague diffuse darkening or very small incipient or vestigial maculations; labrum pale yellow to amber brown; tarsi reddish brown to nearly black, apex of terminal tarsomere distinctly paler, yellow or orange to reddish brown; presectoral area with 8 cells; basal cell of HW costal area almost completely devoid of dark color and sclerotization; male abdomen length between two thirds and full length of wings folded over back; T1 setae moderately to very dense, long, wispy, golden brown; GPC dorsal notch present; linguella a weakly expanded membranous locus bearing several, but not numerous, setae.

Distribution.—Worldwide in temperate, subtropical and tropical latitudes, except absent in Europe and Australia; Western Hemisphere: U.S. (approx. south of 39th parallel) to northern Argentina (approx. north of 34th parallel), absent in Chile and most of Caribbean.

Discussion.—Although a few of its taxa are highly derived, there are many indications that the group of entire eyed owlfly genera occurring in the Western Hemisphere represents a monophyletic unit (and thus tribal status), including geographic isolation and unique common morphological features. The synapomorphies presented above, taken from the cladistic analysis, indicate numerous shared traits observed in this study that may may represent tribal-level apomorphies, if these taxa continue to be supported as monophyletic. Higher level analysis of the Haplogleniinae that includes deeper generic sampling from outside the Western Hemisphere is needed to confirm this. See the 'Cladistic analysis' above for further discussion.

Included genera.—*Amoea* Lefèbvre, 1842; *Neascalobyas* n. gen.; *Ascalobyas* Penny, 1982; *Haploglenius* Burmeister, 1839.

Key to the genera of* Haplogleniinae *of the Western Hemisphere

(adult males and females)

1. Pleuron with a pair of oblique yellow stripes, each stripe running anteroventrad from wing base to subtending coxa [Mexico to Argentina] .... ***Haploglenius* Burmeister** (part)

1'. Pleuron pattern variable, but without pair of oblique yellow stripes 2

2. Wing bases narrowed, concave; FW anal angle developed into a process; antennae with verticils [U.S. to Honduras, Colombia, Venezuela] .... ***Haploglenius* Burmeister** (part)

2'. Wing bases not narrowed, convex; FW anal angle not developed into a process; antennae without verticils 3

3. Antennae reaching past second fork of Rs in spread specimens [U.S. to Argentina] .... ***Amoea*** Lefèbvre

3'. Antennae not reaching past second fork of Rs in spread specimens 4

4. FW costal area devoid of pigment (occasionally lightly tinged); HW anterior and posterior margin mesally narrowed, essentially parallel; HW apex nearly symmetrical, rounded [Costa Rica, Panama; Brazil, French Guiana, Peru, Ecuador; Venezuela] .... ***Neascalobyas* n. gen.**

4'. FW costal area distinctly darkened; HW anterior and posterior margins mesally convergent apicad; HW apex subacute, slightly asymmetrical [U.S. to Argentina] .... ***Ascalobyas* Rambur**

Genus **Amoea** *Lefèbvre, 1842*

Type species *Ascalaphus subcostatus* Burmeister, 1839, by monotypy

Amoea Lefèbvre 1842

—Lefèbvre 1842.04.?? r#3666: 6 {TSP: *Ascalaphus subcostatus* Burmeister. TS: monotypy (3 additional new species are indicated but unnamed). D, IS, K.}

—Walker 1853 r#6194: 446 {JSYN (of *Ascalaphus* Fabricius).}

—Hagen 1866 r#460: 379 {IS, L, SYN}

—McLachlan 1871.09.14 r#353: 219, 233, 234 {JSYN (of *Haploglenius* Burmeister)}

—van der Weele 1909.01.05 r#420: 33 {DIS, IS, MON, RD, SYN, TS}

—Navás 1912b.10.31 r#542: 209 {D, IS, K}

—Navás 1913 r#1207: 48 {D, IS, K}

—Williner 1945 r#6292: 427 {D, IS}

—Orfila 1949 r#5020: 188, 190 {DIS, TSP}

—Shetlar 1977 r#5727: 76, 83 {Ph.D. dissertation, nomenclatural acts invalid: DIS, GD, IS, SYN, TSP, RD}

—Henry 1978a r#2880: 9 {DIS}

—Penny 1978.09.15 r#5098: 11 {IS, L}

—Henry 1978b r#2878: 80, fig. 1 {PHY}

—Penny 1982a r#5105: 395 {DIS, GD, IS, MOR, SYN, TSP}

—Penny 1982b r#5103: 616 {D, DIS, GD, IS, MOR, SYN, TSP}

—Oswald and Penny 1991.12.02 r#7138: 8 {L, SYN, TSP}

—Tjeder 1992 r#7246: 38 {IMS, MOR}

—Penny 2002.10.21 r#10230: 177 {D, GD, IS, K, MOR}

Episperches Gerstaecker 1894

—Gerstaecker 1894 r#2559: 98 {TSP: not designated. TS: not indicated. OD, D, GD, IS, MOR}

—van der Weele 1904 r#397: 203, 204 {DIS, MOR}

—van der Weele 1906 r#404: 227 {DIS, MOR}

—van der Weele 1909.01.05 r#420: 37 {D, DIS, GD, IS, RD}

—Navás 1912b.10.31 r#542: 210 {D, IS, K}

—Navás 1912c.12.30 r#1158: 56 {TSP (*Ascalaphus iniquus* Walker)}

—Navás 1913 r#1207: 50 {D, IS, K}

—Orfila 1949 r#5020: 188 {DIS}

—New 1971 r#4457: 75, fig. 2 {IMS, MOR}

—Henry 1972 r#2875: 2, 19, 20 {IMS, MOR}

—Shetlar 1977 r#5727: 76 {Ph.D. dissertation, nomenclatural acts invalid: DIS, JSYN (of *Amoea* Lefèbvre), MOR}

—Henry 1978a r#2880: 9, 17 {DIS, IMS, MOR}

—Penny 1978.09.15 r#5098: 12 {IS, L}

—Henry 1978b r#2878: 75, 80, 81, fig. 1 {DIS, IMS, MOR, PHY}

—Penny 1982a r#5105: 395 {DIS, JSYN (of *Amoea* Lefèbvre), MOR, TSP (*Episperches vacuus* Gerstaecker; incorrect designation—see Oswald and Penny 1991)}

—Oswald and Penny 1991.12.02 r#7138: 8, 23 {JSYN (of *Amoea* Lefèbvre), SYN, TSP}

—Tjeder 1992 r#7246: 38 {IMS, MOR}

<u>Etymology and nomenclatural notes</u>.—*Amoea*: Amo- (Latin), 'to love physically or passionately', or 'to be obligated to' + -ea (Latin), 'having the quality of', = 'loving', 'having loved', or 'devoted'. According to Oswald (unpublished data), this name may have been created "in allusion to the love of Acheron and Orphne, parents of Ascalaphus [=Askalaphos] in Gr. mythology".

Diagnosis.—Antennae extending beyond second fork of FW Rs in spread specimens. Wing basiposterior margins convex, FW anal angle undeveloped into a process. Wings of most species completely lacking pigment (though sometimes costal and subcostal area in a few species very faintly tinted, and some individuals melanistic), except for pterostigmata, whose membranes range from clear to cream to brownish; pterostigma veinlets brown. FW presectoral area with 8 (rarely 9) cells. HW anal area with two complete rows of cells. Thoracic pleuron lacking a pair of oblique broad yellow stripes. Males: prothoracic valve undeveloped; thorax of several species completely covered with pruinescence; pelta narrow spindle-shaped; S3 with an anterior marginal yellow maculation.

Synapomorphies.—pteronotum with at least some yellow maculations, sometimes distinct.

Distribution.—Mexico to Argentina, with a few presumably incidental records in the U.S. (Louisiana, Utah).

Description.—

Head. Breadth at widest point (of eyes) more or less coequal to or slightly greater than that of mesothorax at wing base. Occiput usually patterned, but pattern variable and often obscured. Vertex nearly flat dorsally or very weakly arched but not bilobed; epicranial suture distinct; vertex plates often hard to see, more or less flush with surface, texture granular and glossy; anterosagittal plate expressed as very slender parasagittal bands bordering epicranial suture and diverging posteriorly; posterosagittal plate slightly broader than narrow anterior portion of anterior plate, length greater than three times width, shape cordate or narrowly almond-like, but well divided by epicranial suture into two hemispheres; anterolateral plate positioned laterad of anterosagittal plate, contiguous with orbital sclerite, crescent-shaped, with arms directed mesad; posterolateral plate positioned laterad of posterosagittal plate, contiguous with orbital sclerite, irregularly donut- or claw-shaped; setae at least somewhat dense near antennae, becoming more sparse dorsally and posteriorly, intermediately long. Extra-torular sclerites each a narrow band, mesally fused at base of antennae. Paraocular band glabrous. Frons transversely slightly swollen. Setosity of mouthparts as in other owlflies (e.g., *Allocormodes*). Eyes entire, sometimes slightly larger in ventral half, at least very slightly dorsoventrally oblong, dividing sulcus absent, but usually with a hint of a dorsoventral mesal flattening. Antennae flagellomeres with shape undifferentiated, verticils absent; clubs pyriform with apices rounded, covered in fine setae.

Thorax. Dorsal cervical plate swollen, weakly offset from cervical membrane, bearing long, slender setae. In males of some species, pruinescence often nearly completely covering thoracic sclerites. *Pronotum.* Anterior flange narrow, very briefly produced dorsad, rising highest sublaterally. Medial transverse band narrow, posterolateral knob produced, apically bulbous. Posterior flange produced somewhat posteriorly, distal margin covering mesoacrotergite, sublaterally bent but not articulated, ventral surface membranous, membrane contiguous with mesonotal acrotergite, white coating absent. *Pteronotum.* Pattern variable, usually earthy brown with a few diffuse yellow or orange maculations. *Pleuron.* Color pattern variable, often variegated brown and yellow, frequently differing slightly in males and females, several species with a broad yellow subalar stripe.

Legs. Color patterning variable; femora and tibiae with long, stiff, black setae. Tibial only very weakly curved, almost straight, posterior spur longer than anterior one, overall lengths varying slightly among species.

Wings. Elongate and somewhat broad; HW pre-Mp_1 area margin in most species slightly expanded in females and greatly expanded in males. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined. Pterostigma membrane devoid of pigment to cream or pale brown, translucent to opaque, distal margin of pigment straight; veins often thickened and appearing slightly margined. Deltus with pigment distribution variable and sometimes diagnostic. Presectoral area with eight cells. Anal area hind margin convex, anal angle not developed into a process, a single cell row distad of Cup + 1a, second basal cell always divided by a crossvein, but remaining cells usually undivided. *Color and patterning.* Membranes of entire wing hyaline, usually colorless, but sometimes with a very slight dusky hue, particularly in males, and sometimes slightly tinged with pale brown in costal and subcostal areas; some males of one species with wings melanistic, dark. HW. Anal area with two rows of cells, marginal row with cells rarely divided by crossveins.

Abdomen. In males, reaching to pterostigma or slightly past when wings folded back; in females, usually not reaching to pterostigma, much shorter. *Tergum*. Base color dull dark brown, patterns often subtle or obscured, parasagittal stripes and imbedded spots often expressed, more often in females; in females tergum distad of T2 devoid of long setae; in males, tergum setosity variable and diagnostic. *Sternum*. Brown to yellow; surfaces beyond S3 devoid of long setae. *Pleural membrane*. In females, mostly devoid of long setae; in males, setosity variable among species and diagnostic.

Male terminalia. In unmacerated specimens GPC and apices of pulvini everted or not. Ectoprocts simple. S9 apical margin obtusely angled. Pulvini size and length of its setae somewhat variable. GPC rather weakly sclerotized; in lateral view dorsal notch present or absent, dorsal and ventral margins usually convergent apicad; in ventral view width variable. Parameres sclerotized, in lateral view unproduced, in ventral view simple, appearing more or less like cloven hooves, but shape somewhat variable. Pelta simple, very narrowly to more broadly almond-shaped.

Female terminalia. Ectoprocts simple. Ventrovalvae elongate and somewhat narrow. Distivalvae in lateral view subtriangular. Linguella weakly produced and poorly sclerotized, bearing several short, slender, stiff, setae. Interdental space shape somewhat variable, glabrous. Interdens sclerotized, somewhat small, cone-, nipple- or pin-like.

Discussion.—Although a specimen (JRJ_00237) was determined to probably represent the female of *chlorops*, its thorax coloration is obscured by oils and crucial diagnostic features are difficult to discern, and so it was not included in the key to females.

Included species.—*arenosa* (Walker); *chlorops* (Blanchard); *flavitaenia* n. sp.; *immaculata* (Olivier); *impediens* (Walker); *iniqua* (Walker); *latipennis* (Navás); *nivea* Navás; *periculosa* n. sp.; *vacua* (Gerstaecker).

Removed from *Amoea*.—*molinai* Navás; *electrodominicana* Grimaldi and Engel† (see discussion at end of treatment of *Amoea* spp.).

Key to the species of **Amoea,** *adult males*

1. Lacking a well-defined and uninterrupted yellow subalar stripe (pleuron often obscured by pruinescence in some species) 2

1'. A broad, well-defined, uninterrupted yellow subalar stripe present, stripe margin ventrally at least somewhat regular and distinct 8

2(1). Pleural membrane of abdominal segments 3-7 with a very dense coat of pale golden or dark brown setae, gradually thinning out toward distal segments; thorax often pruinescent 3

2'. Pleural membrane of abdominal segments 3-7 largely glabrous; thorax only rarely with some pruinescence 6

3(2). HW hind margin in proximal half of wing weakly expanded, hardly broader than wing at midpoint; pleuron largely evenly yellow; thorax not pruinescent; T1 plates each bearing a dense patch of long, erect, dorsomesally directed, wispy white setae; some individuals melanistic, with very dark wings [Bolivia, Ecuador, Paraguay, Peru] .... ***nivea*** **Navás**

3'. HW hind margin in proximal half considerably expanded, considerably broader than wing at midpoint; pleuron variegated with brown and yellow; thorax pruinescent or not; T1 plates not bearing long, erect, wispy white setae 4

4(3’). FW: deltus with gap or yellowing of pigment at junction of R and 1r-m; thoracic pleuron with no hint of a yellow subalar stripe; abdominal tergal pattern (diffuse parasagittal cinnamon-colored stripes imbedded with a small diffuse dark macula on mesal and distal part of each tergite) usually present and at least somewhat well-defined [Eastern Mexico to Costa Rica, Utah] .... ***vacua*** **Gerstaecker**

4’. FW: deltus completely filled with brown pigment, often darker near junction of R and 1r-m; pleuron sometimes with the hint of a yellow subalar stripe; abdominal tergal pattern usually obscured or absent 5

5(4’). Subcostal veinlet 2 to approximately 7 or 8 margined, sometimes thinly and diffusely, with brown pigment; often most other veins, veinlets and crossveins thinly and diffusely margined, giving the wing a slightly darker appearance; thorax often pruinescent; overall appearance of thorax medium to pale brown and yellow [Costa Rica north to western Mexico] .... ***latipennis*** **Navás**

5’. Subcostal veinlets, as well as other veins, veinlets and crossveins, unmargined; thorax not pruinescent; overall appearance of thorax pale to dark gray [Bolivia, Brazil, Guyana, French Guiana] .... ***periculosa*** **n. sp.**

6(2’). Species with larger wings (FW >35 mm) [eastern Brazil] .... ***immaculata*** **Olivier**

6’. Species with medium-sized wings (FW <34 mm) 7

7 (6’). Pronotum posterior flange dorsally yellow to orange, with a dark brown sagittal line and distal margin often also dark brown; pteronotum with several distinct yellow to orange maculations; subcostal and sometimes costal areas often slightly tinted; HW basal posterior margin (anal + posterior medial + anterior medial areas) only slightly expanded [Brazil] .... ***chlorops*** **(Blanchard)**

7’. Flange evenly orange to brown, only very rarely with a dark sagittal line, and pteronotum with yellow or orange maculations absent or very weakly expressed; costal and subcostal areas devoid of pigment; HW basal posterior margin (anal + posterior medial + anterior medial areas) greatly expanded [Brazil] .... ***iniqua*** **Walker**

8(1’). Paired sublateral notal stripes absent [Costa Rica, Mexico, Panama, U.S.: Louisiana] .... ***flavitaenia*** **n. sp.**

8’. Notal stripes present 9

9(8’). Notal stripes very narrow, sharply defined; brown stripe subtending yellow subalar stripe present, broad, well-developed; setae of subalar stripe white, wispy, medium length to long but denser and longer than setae on more ventral parts of pleuron and conspicuous in lateral view [Brazil, Peru] .... ***impediens*** **Walker**

9’. Notal stripes only somewhat narrow, often somewhat diffused; brown stripe subtending subalar stripe poorly-developed, narrow, color blotchy; setae of subalar yellow stripe white, wispy, medium length, sparse to intermediately dense but consistent in density with that on more ventral parts of pleuron, only moderately conspicuous in lateral view [Argentina, Bolivia, Brazil, Paraguay] .... ***arenosa*** **Walker**

Key to the species of* Amoea*, adult females

(not included: *nivea*)

1. Broad, uninterrupted yellow subalar stripe present, stripe margin ventrally at least somewhat defined 2

1’. Lacking a well-defined and uninterrupted yellow subalar stripe 6

2(1). Parasagittal pale notal stripes present 3

2’. Notal stripes absent 4

3(2). Notal stripes very narrow, sharply defined; brown stripe subtending yellow subalar stripe present, broad, well-developed; setae of subalar stripe white, wispy, medium length to long but conspicuously denser and longer than setae on more ventral parts of pleuron [Brazil, Peru] .... ***impediens*** **Walker**

3’. Notal stripes only somewhat narrow, often somewhat diffused; brown stripe subtending subalar stripe poorly-developed, narrow, color blotchy; setae of subalar yellow stripe white, wispy, medium length, sparse to intermediately dense, but consistent in density with that on more ventral parts of pleuron, and only moderately conspicuous in lateral view [Argentina, Bolivia, Brazil, Paraguay] .... ***arenosa* Walker**

4(2’). Ventral margin of subalar stripe irregular and at least somewhat weakly differentiated from variegated pattern below; abdominal tergum with narrow cinnamon-colored parasagittal stripes along full length; each tergite with a small, somewhat diffuse, round, dark brown spot embedded in stripe just anterad of midpoint and another immediately anterad of posterior margin [Costa Rica north to western Mexico] .... ***latipennis* Navás**

4’. Ventral margin of subalar stripe essentially straight and well-defined; abdominal tergum usually evenly brown, but if parasagittal stripes present, these often very diffuse and irregular from tergite to tergite, or broad, blotchy and orangish; brown spots sometimes present anterad of posterior margin, but slightly larger and very diffuse 5

5(4’). Colors of notum and pleuron with yellows dark cream to yolk, browns a dark plum color; dorsal surfaces of pro- and mesothoracic tibia dark blackish-brown; basal sclerites of wings very dark brown with yellow highlights, and basal sclerites membranes often opaque; wing venation dark, almost black in some specimens [Bolivia, Brazil, Guyana, French Guiana] .... ***periculosa* n. sp.**

5’. Colors of notum and pleuron with yellows cream to yolk, browns only medium honey brown to moderately dark; tibia dorsal surfaces smoky yellow and obscure to evenly medium brown; basal sclerites of wings pale to medium brown, membranes not opaque; wing venation somewhat dark to pale brown or even yellowish [Costa Rica, Mexico, Panama, U.S.: Louisiana] .... ***flavitaenia*** **n. sp.**

6(1’). Species with larger wings (FW>38 mm); subcostal and costal areas often slightly tinted [eastern Brazil] .... ***immaculata*** **Olivier**

6’. Species with medium-sized wings (FW <37 mm); costal and subcostal areas tinted or not 7

7(6’). Deltus completely filled with brown or yellowish brown pigment, often darker near junction of R and 1r-m 8

7’. FW basal cell not completely filled with brown pigment: either mostly filled with pigment but absent or yellowish at junction of R and Mp, or very lightly tinged with brownish pigment, or devoid of pigment altogether 9

8(7). Subcostal veinlet 2 to approximately 7 or 8 margined with brown pigment, sometimes only thinly and diffusely; often most other veins, veinlets and crossveins thinly and diffusely margined, giving the wing a slightly darker appearance; thoracic pleuron strongly variegated, colors subdued, yellow pigment sometimes aggregating into the hint of a subalar stripe [Costa Rica north to western Mexico] .... ***latipennis* Navás**

8'. Subcostal veinlets and other wing veins not margined; thoracic pleuron strongly variegated brown and yellow, colors not subdued, with no hint of a subalar stripe [Brazil] .... ***chlorops* (Blanchard)**

9(7'). Deltus mostly completely filled with brown pigment, but pigment absent or distinctly yellowed and thin at junction of R and 1r-m; pronotum posterior flange orange, with a diffuse brown narrow sagittal stripe and distal margin; pteronotum medium to dark brown, with yellow maculations present, diffuse but distinct [Eastern Mexico to Costa Rica, Utah] .... ***vacua* Gerstaecker**

9'. Deltus devoid of, or very lightly tinged with brown pigment; pronotum posterior flange evenly dark brown; pteronotum evenly honey brown to dark brown, with yellow maculations usually very diffuse or absent [Brazil] .... ***iniqua* Walker**

Amoea arenosa *(Walker, 1853)*

(A3 Figs. 2–3, 79)

Ascalaphus arenosus Walker, 1853

—Walker 1853 r#6194: 450 {OD: sex not indicated [♂], D. TS: not indicated [holotype by explicit monotypy]. TL: “Brazil”. TR: BMNH. Type specimen examined (see “Type material examined” below).}

—Hagen 1861.07.?? r#455: 327 {GD, L, SYN}

—Hagen 1866 r#460: 381 {L, SYN}

—McLachlan 1871.09.14 r#353: 234, 237 {MOR, SYN}

—van der Weele 1909.01.05 r#420: 41 {SYN}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 12 {SYN}

—Penny 1982b r#5103: 616, 619 {JSYN (of *Ascalaphus iniquus* Walker), MOR, TR}

Haploglenius arenosus (Walker, 1853)

—Hagen 1866 r#460: 381, 406 {L, NC, SYN}

—McLachlan 1871.09.14 r#353: 237 {D, DIS, GD, MOR, SYN}

—van der Weele 1909.01.05 r#420: 41 {SYN}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 12 {SYN}

—Penny 1982b r#5103: 616 {JSYN (of *Ascalaphus iniquus* Walker)}

Episperches arenosus (Walker, 1853)

—van der Weele 1909.01.05 r#420: 41, fig. 14 {GD, NC, RD: ♂♀, SR, SYN}

—Navás 1911 r#535: 24 {SR}

—Navás 1912b.10.31 r#542: 211 {D, GD, K}

—Navás 1913 r#1207: 51 {D, GD, K}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—New 1971 r#4457: 76, table 1 {IMS, MOR}

—Penny 1978.09.15 r#5098: 12 {GD, L, SYN}

—Penny 1982a r#5105: 395 {MOR}

—Penny 1982b r#5103: 616 {JSYN (of *Ascalaphus iniquus* Walker)}

Amoea loretana Navás, 1930 **new synonym**

—Navás 1930 r#882: 126, fig. 21 {OD: ♂, D. TS: not indicated [holotype by explicit monotypy]. TL: "República Argentina: Loreto, Misiones". TR: not indicated [MACN—see Williner 1945]. Type specimen not examined (see "Discussion" below).}

—Williner 1945 r#6292: 427 {L, SR, TR}

—Penny 1978.09.15 r#5098: 11 {GD, L}

Amoea fulva Navás, 1931 **new synonym**

—Navás 1931 r#892: 60 {OD: ♀. TS: not indicated [holotype]. TL: "San Bernardino, Paraguay". TR: ZMUH (probably destroyed in WWII—see Oswald 2013a). Type specimen not examined (see "Discussion" below).}

—Penny 1978.09.15 r#5098: 11 {GD, L}

<u>Etymology and nomenclatural notes</u>.—*arenosa*: arenosus (Latin), 'full of sand'. The entire dorsum of the type specimen (vertex, notum and tergum) is covered in sandy-white colored very fine particulate matter; this coating is somewhat reminiscent of pruinescence, but no other specimens examined exhibited this feature, and the coating may just be dust. The specimen is overall very dirty, with larger grains and particles imbedded in the body setae and on the wings. No doubt these qualities of the specimen led to Walker's name selection.

Diagnosis.—Pteronotal parasagittal stripes present, usually somewhat broad and sometimes weakly defined. Subalar stripe present, well-developed, yellow; subalar stripe setae white, only moderately long and somewhat dense, not differentiated from that on remainder of pleuron; venter of subalar stripe bordered by brown stripe, but this poorly defined ventrally, broader and darker in females, very narrow and irregular in males.

Males: not pruinescent; HW axillary cord setae grayish yellow to brown, only moderately thick.

Autapomorphies.—basal cell of HW costal area almost completely devoid of dark color and sclerotization.

Distribution.—Argentina, Bolivia, Brazil; Paraguay.

Description.—

Size (mm). Male: length of body 25–32, abdomen 16–21, forewing 26–29, hind wing 24–25, antennae 17–18. Female: length of body 28–29, abdomen 18–19, forewing 32–35, hind wing 29–30, antennae 17–18.

Head. Breadth more or less coequal to that of mesothorax. Occiput with irregular and often obscured reddish to dull brown and diffuse yellow maculations. Vertex sandy to reddish brown, sometimes dull yellowish; anterosagittal plate bands dark brown, posterior arms short; posterosagittal plate cordate; setae rather dense near antennae, mixed orangish-yellow and black anteriorly and dorsally, transitioning to yellow posteriorly. Extra-torular sclerites dusky orange to dark brown, often concolorous with frons. Paraocular band more or less concolorous with frons, often paler to yellowish lateroventrally. Frons medium dusky orange; setae moderately dense, mixed orangish-yellow and black. Clypeus yellow to dusky orangish-brown, reddish-brown sagittal line sometimes present, some small or narrow diffuse reddish to brown maculations sometimes present laterally. Labrum color highly variable, often concolorous with clypeus, sometimes becoming darker brown or paler yellow. Mandibles dull dark yellow basally, transitioning to very dark reddish-brown apically. Labium yellow to orangish, with a thin dark brown sagittal line. Eyes in anterior view symmetrically round, in lateral view very slightly larger in ventral half. Antennae flagellomere internodes yellowish to reddish brown, nodes dark reddish brown; clubs medium to dark brown, often with a diffuse broad yellow stripe on anterior face.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, pale yellow setae. Cervical sclerite evenly dark brown. *Pronotum.* Posterior flange posterior margin barely covering mesoacrotergite. Pronotum coloration more or less evenly medium to somewhat dark brown, darker laterally, posterior flange dorsomesally often yellow or orangish, with posterior margin laterally yellowish, mesal margin dark brown, and a narrow diffuse dark brown sagittal stripe present. All surfaces with medium to somewhat long, slender, mixed pale yellow and brown setae. *Pteronotum*. Base color sandy to dark brown, with intermediately broad, sublateral, often diffuse, orangish-yellow to pale brown stripes running longitudinally from anterolateral surface of mesoprescutum to posterolateral surface of metascutellum, slightly convergent posterad, yellow color present often along posterior surface of meso- and metascutellum; velvety spots of metascutum dark brown, darker than other surfaces of sclerite; entire surface of pteronotum covered with intermediately dense, somewhat short, slender, pale yellow to brownish setae, setae somewhat denser and white on lateral surface of mesoprescutum, lateroposterior corner of mesoscutellum, lateral surface of metascutum, and lateral and posterior surfaces of metascutellum. *Pleuron* with yellow color aggregated along sclerites subtending wing bases and forming a broad yellow subalar stripe, surfaces subtending stripe somewhat variegated brown and yellow, but with brown color aggregated into a somewhat irregular narrow longitudinal stripe, posterior surfaces of coxae and meso- and metakatepimeron dark brown, all surfaces more or less evenly covered with a somewhat dense coat of intermediately long, very slender, pale yellow to white setae.

Legs. Femora and tibiae more or less orangish-yellow, sometimes more dusky to reddish-brown, particularly on dorsal and anterolateral surfaces of pro- and mesothoracic legs and on anterolateral surfaces of metathoracic tibia. Tarsi reddish to orangish brown, occasionally dark brown, tibial spurs only very weakly curved, almost straight, not extending past apex of second tarsomere, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, pale yellow setae; antennal comb setae predominately golden, black distally.

Wings. Dimension and shape. Intermediately broad, apically rounded. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal. Pterostigma with four to six forked and unforked brown veinlets; membrane pale cream yellow, sometimes weakly opaque; veins often slightly thickened and appearing very thinly margined. Deltus often completely lacking pigment, sometimes translucent yellowish, rarely anteromesally darkening to brown. Presectoral area with eight cells. Rs with six forks. Mp_2 + Cua_1 evenly curving toward hind margin in distal portion. Cubital area with ca. seven to nine irregular but more or less complete rows of cells. Cubital triangle distal domain with one to three, usually two, cells . Anal area cell row with cells undivided by crossveins. *Color and patterning.* Venation pale to moderately dark brown, usually medium brown. Membranes of wing completely lacking pigment. HW. As in forewing except as follows. Mp_2 fork angle nearly 90°. Medial triangle distal domain with two to three (usually two) cells. Pre-Cup axillary disk brown to dark brown, distal margin devoid of pigment to slightly yellowish. Pre-Mp_1 area margin expanded, slightly more so in males. Anal area with two rows of undivided cells.

Abdomen. Not reaching to pterostigma when wings folded back, usually much shorter. *Tergum*. Base color dull dark brown, a pair of broad pale yellow to orangish parasagittal stripes often expressed along full length and separated by a narrow dark brown sagittal line, pale stripes sometimes with numerous small dark flecks, a pair of small, diffuse, very dark brown parasagittal spots positioned immediately anterad of posterior margin of T4 to T8; In females, T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, pale golden setae, remainder of tergum devoid of long setae, in males, T1 with a dense covering of long, slender, pale yellow setae, T2 to T6 with a dense covering of very short, slender, wispy, pale yellow setae. *Sternum*. Base color dark brown, S1 proximal membrane and anteromesal portion of S2 predominately diffusely yellow, a medium large, round diffuse yellow macula on anterior portion of T3, in females, ventral surfaces of S3 to S7 often becoming largely yellow, especially on distal two or three sternites; surfaces mostly devoid of long setae, some intermediately long, wispy, pale gold and dark brown setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3. *Pleural membrane*. In females, mostly devoid of long setae, a few wispy brown or golden setae on membrane of segment 2; in males, membrane of segment 2 with long, wispy, golden brown setae, membrane of segments 3 to 6 with a dense coat of short, wispy, pale yellow or golden setae.

Male terminalia. Unmacerated specimens. GPC usually not everted, pulvini not visible. *Macerated specimens.* S9 apical margin essentially straight, not angled. Pulvini somewhat small, weakly sclerotized, two to three times as long as width at base, bearing numerous intermediately long, slender, brown setae. GPC weakly sclerotized; in lateral view dorsally more or less entire, dorsal notch essentially absent, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view somewhat broad laterally. Parameres sclerotized, in lateral view unproduced, in ventral view simple, appearing like cloven hooves of a deer, but not curved, proximal margins weakly differentiated. Pelta somewhat sclerotized, very narrowly almond-shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distivalvae yellow, ectoprocts mostly yellow. *Macerated specimens.* Ventrovalvae elongate and somewhat narrow, subtriangular, length ca. two times width. Distivalvae in lateral view subtriangular. Linguella weakly produced, poorly sclerotized, bearing several short, slender, stiff, setae. Interdental space subtriangular, glabrous. Interdens sclerotized, somewhat small, cylindrical, nipple-like, apex with a few very short slender setae.

Variation. The pattern of the pronotum is not always well expressed; the pteronotal stripes are sometimes narrow or diffuse.

Type material examined.—*Holotype* (A3 Fig. 2), male, Brazil, in BMNH collection: "Type /// Brazil /// arenosus /// arenosus Wlk /// JRJ_01626". Condition: fair; antennae missing; a wooden splint inserted inside abdomen along its length. In his original description, which was based on a single specimen (in his descriptions Walker lettered his specimens examined thusly: "a. …, b. …"), Walker (1853) states that the abdomen is slightly longer than the HW; however, in the type specimen, the abdomen is unnaturally stretched out by the splint (a feature of many mounted type specimens retained in the BMNH). It is not clear if it was Walker or some other worker (Walker states the specimen came from the collection of Mr. Stevens) who employed this mounting technique, which, unfortunately, renders dissection nearly impossible.

Additional material examined.—*Argentina*: (FSCA: 1 ♀, JRJ_00215). *Bolivia*: Santa Cruz (CMNH: 2 ♂♂, JRJ_00202, JRJ_00203, 2 ♀♀, JRJ_00204, JRJ_00205 [A3 Fig. 3]). *Brazil*: Amazonas (MNHN: 1 ♀, JRJ_01633); Minas Gerais (UMSP: 1 ♀, JRJ_00211); Rondônia (FSCA: 4 ♂♂, JRJ_00207, JRJ_00208, JRJ_00209, JRJ_00210); locality unknown (BMNH: 1 ♀, JRJ_01621). *Paraguay*: Central (MFNB: 1 ♂, JRJ_00206). *South America*: locality unknown (MFNB: 1 ♂, JRJ_01701).

Morphology, biology and ecology.—Specimens were collected at elevations of 450 and 800 m. A small series of males was collected at MV and UV lights in Rondônia.

Discussion.—The notal stripes are rather dull and diffuse in some specimens, and this appears to have led to confusion about the identity of the species and the creation of a few synonyms by Navás.

Amoea chlorops *(Blanchard in Blanchard and Brullé, 1845)*

(A3 Figs. 4–7, 80)

Ascalaphus chlorops Blanchard, 1845

—Blanchard in Blanchard and Brullé 1845 r#1595: 218, pl. XXVIII, fig. 8 {OD: ♀. TS: not indicated [holotype]. TL: "Santa Cruz (Bolivia)". TR: not indicated [MNHN, but lost—see van der Weele 1909: 37]. Type specimen not examined (see "Discussion" below).}

—Walker 1853 r#6194: 453 {RD: ♀ (copied from OD), SYN, TL}

—Hagen 1861.07.?? r#455: 326 {GD, L}

—Hagen 1866 r#460: 382 {L, SYN}

—McLachlan 1871.09.14 r#353: 248 {SYN}

—van der Weele 1909.01.05 r#420: 35 {SYN}

—Williner 1945 r#6292: 427 {SYN}

—Penny 1978.09.15 r#5098: 11 {SYN}

Suhpalacsa chlorops (Blanchard, 1845)

—Hagen 1866 r#460: 382, 461 {NC [as "*Suphalasca* [sic] *chlorops* Blanch."}

Ulula chlorops (Blanchard, 1845)

—McLachlan 1871.09.14 r#353: 248 {GD, NC, DIS}

—van der Weele 1909.01.05 r#420: 35 {SYN}

Amoea chlorops (Blanchard, 1845)

—van der Weele 1909.01.05 r#420: 35, fig. 10 {DIS, GD, NC, RD: ♂♀, SYN}

—Navás 1912b.10.31 r#542: 210 {D, GD, K}

—Navás 1913 r#1207: 49 { D, GD, K}

—Navás 1930 r#882: 127 {MOR}

—Williner 1945 r#6292: 426 {SYN}

—Penny 1978.09.15 r#5098: 11 {GD, L, SYN}

Ululaus [sic] *chlorops* McLachlan 1871"

—Williner 1945 r#6292: 427 {SYN}

—Penny 1978.09.15 r#5098: 11 {SYN}

Etymology and nomenclatural notes.—*chlorops*: chloros (Greek), 'green' + –ops (Greek) 'eye', = 'green eyes'. Named by Blanchard for the green eyes of the type specimen.

Diagnosis.—Pteronotal parasagittal stripes absent, but notum with at least some with distinct/sharp yellow maculations, predominately brown, setae only moderately dense and long, golden. Subalar stripe absent; pleuron strongly variegated brown and yellow, colors not subdued, sometimes predominantly brown. Subcostal area sometimes faintly tinted. Males: notum slightly pruinescent or not at all; HW base slightly less expanded and expanded area slightly broader than in other species; abdominal tergum and pleural membrane setae extremely sparse, with a very few wispy ones on T1.

Autapomorphies.—pronotum and mesoprescutum setae of males somewhat sparse to only intermediately dense, only moderately long, very pale yellow to white.

Distribution.—Bolivia, southeastern Brazil.

Description.—

Size (mm). Male: length of body 25–33, abdomen 17–23, forewing 30–34, hind wing 26–31, antennae 18–19. Female: length of body 26–32, abdomen 19–23, forewing 34–38, hind wing 30–34, antennae 18–20.

Head. Breadth slightly superequal to that of mesothorax. Occiput with an irregular and often obscured pattern of brown and yellow maculations. Vertex sandy to dark brown; vertex plates dark brown to dull grayish-yellow; setae somewhat dense near antennae, pale yellow with tips dark brown and some dark brown setae mixed in dorsally, transitioning to just pale golden yellow or dull brownish posteriorly. Extra-torular sclerites dark brown mesally, dusky orange laterally, often concolorous with prefrons and dorsal most portions of paraocular band laterad of antennal bases.

Paraocular band dark brown laterad of antennae, transitioning to yellow adjacent to frons. Frons dark brown in dorsal third, transitioning to dusky pale yellow or orangish; setae somewhat dense, pale or golden-yellow, a few dark brown ones dorsolaterally. Clypeus pale to dusky yellow, laterally often with very diffuse reddish-brown maculations, rarely with a dark brown sagittal line. Labrum concolorous with mesal portion of clypeus. Mandibles concolorous with labrum basally, transitioning to very dark reddish-brown apically. Labium pale to dusky yellow, with a thin dark brown sagittal line. Eyes somewhat larger in ventral half. Antennae flagellomere internodes yellowish to reddish brown, nodes dark reddish brown, rarely paler subapically before node darkens, nodes in apical fourth of flagellum with a few short apical setae; clubs dark brown, often with anterior face diffusely yellowish or orange.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, pale golden setae. Cervical sclerite mostly evenly dark brown, proximoventrally yellowish. *Pronotum.* Posterior flange posteror margin not quite or just barely covering mesoacrotergite. Coloration of anterior flange and medial transverse band more or less dark brown, posterior flange predominately orange, posterior margin dark brown, this contiguous with a diffuse dark brown sagittal line. All surfaces with medium to somewhat long, slender, brown setae. *Pteronotum*. Dark brown, with diffuse yellow or orange maculations on anterolateral faces of mesoprescutum, on mesotegula, sometimes on anterior surfaces of mesoscutellum as sublateral dull orangish teardrop-shaped maculae, on anterolateral and mesal faces of transverse posterior swelling of mesoscutellum, and laterally on metascutellum; velvety spots of metascutum dark brown, darker than other surfaces of sclerite; entire surface of pteronotum covered with somewhat dense, intermediately long, very fine, golden brown setae, setae very slightly denser and longer on posterolateral surfaces of mesoscutum, mesoscutellum, metascutum, and metascutellum. *Pleuron* with color strongly variegated, yolk-yellow and dark brown, colors occasionally slightly duller, but usually rather intense; all surfaces more or less evenly covered with a somewhat dense coat of intermediately long, very slender, pale yellow setae, these sometimes slightly denser and longer on mes- and metanepisternum.

Legs. Femora pale yellow in proximal third, transitioning to dusky brown in distal two-thirds, at least on dorsal surfaces; tibiae pale yellow ventrally, dusky dark brown dorsally and anterolaterally. Tarsi very dark reddish-brown, almost black, terminal tarsomere with apex diffusely pale reddish, tibial spurs only very weakly curved, almost straight, posterior spur longer than anterior one and extending approximately to apex of second tarsomere, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, very pale yellow setae; antennal comb setae golden.

Wings. Dimension and shape. Intermediately broad, apically rounded. *Venation/cells.* FW. Costal area with subcostal veinlets slight inclined, cell width and height more or less coequal in proximal half of wing, cells slightly narrower in distal half. Pterostigma with four to five forked and unforked brown veinlets; membrane pale cream white to slightly brownish, usually translucent but sometimes becoming slightly opaque; veins often thickened and very thinly margined. Deltus usually translucent brownish, sometimes becoming darker and opaque anteriorly. Presectoral area with eight cells, occasionally only seven, rarely nine. Rs with six forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine to ten irregular but more or less complete rows of cells. Cubital triangle distal domain with one or two, often just one, cells . Anal area cell row sometimes with one distal cell divided by a crossvein. *Color and patterning.* Venation pale to moderately dark brown, usually medium brown. Membranes of wing mostly completely lacking pigment, but subcostal area and, less frequently, costal area sometimes weakly tinged with brown color. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with two to three , usually two cells. Pre-Cup axillary disk dark brown, distally translucent to pale yellow. Pre-Mp_1 area margin slightly and broadly expanded in both males and females. Anal area with two rows of cells, marginal row occasionally with one or two distal cells divided by crossveins.

Abdomen. In males reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Base color dull dark brown, parasagittally broadly and diffusely dark orange, each tergite with a broad, diffuse, transverse, dark brown maculation positioned around antecostal scar and another immediately anterad of posterior margin, pattern most well expressed on T3 and T4, often obscured and entire tergum appearing brownish; T1 with some intermediately dense, intermediately long, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. Sometimes evenly dark brown, but sometimes with a pattern beginning to form, as follows. S2 to S4 laterally dark brown, mesally yolk yellow, posterior margin of S3 and S4 with brown pigment forming a broad transverse band, this bisected by a narrow sagittal line of yellow pigment, often a second, rather diffuse, transverse band of brown pigment immediately posterad of sternite midpoint, and a thin diffuse brown sagittal line on mesal portion of sternite, this pattern sometimes weakly expressed on subsequent sternites; surfaces mostly devoid of long setae, some intermediately long, wispy, pale golden setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3. *Pleural membrane*. Mostly devoid of long setae, membrane of segment 2 with some long, wispy, pale golden setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible, ectoprocts dark brown with distal margin narrowly diffusely orange. *Macerated specimens.* Not available.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, apices diffusely yellowish-orange, distivalvae yellowish-orange, ectoprocts distal margin yellowish-orange. *Macerated specimens.* Ventrovalvae elongate and somewhat narrow, subtriangular, length ca. two times width. Distivalvae in lateral view subtriangular. Linguella weakly produced, poorly sclerotized, bearing several short, slender, stiff, setae. Interdental space triangular, glabrous. Interdens sclerotized, somewhat small, nipple-like.

Variation. One male (JRJ_01720) with notum bearing an uneven dusting of pruinescence. Another male (JRJ_00194) with what appears to be pruinescence on metanotum and abdominal tergites T1 to T4, but this could be dust or fine sand.

Type material examined.—Type specimen not available for examination.

Additional material examined.—*Brazil*: Rio de Janiero (MFNB: 1 ♂, JRJ_01720 [A3 Fig. 6]; 1 ♀, JRJ_01721 [A3 Fig. 7]); Rio Grande do Sul (BMNH: 1 ♀, JRJ_01616 [A3 Fig. 5]; MFNB: 1 ♀, JRJ_01703); Santa Catarina (TAMU: 1 ♀, JRJ_00240; UNESP: 1 ♂, JRJ_00236 [A3 Fig. 4]); São Paulo (FSCA: 1 ♀, JRJ_00241).

Morphology, biology and ecology.—One specimen was reportedly collected at elevations from 300 to 500 m. As with *immaculata,* this species appears to occur in southeastern coastal forests of Brazil.

Discussion.—*Ascalaphus chlorops* Blanchard is an enigma. It was described from a single female from Santa Cruz, Bolivia, and the description is very brief: "Testaceo-fuscus, pilosus; thorace, maculis seu vittis obscurioribus; oculis nitidis pallide aureo-viridibus; alis vitreis, nervis fuscis; pedibus pallidis, genubus, tibiarum apice tarsisque piceis. Long. 32 mill., enverg., 62 mill." Blanchard provided a beautiful drawing of the specimen which has some degree of detail in the wing venation (indicating a match to *Amoea* spp.), but the shape in the run of the veins and wing margins is a bit stylized and inaccurate, and the dorsal view provides only a limited amount of additional diagnostic information.

Van der Weele (1909) was the first author to redescribe *chlorops*. He based his concept on a handful of specimens from southeastern Brazil and southern Paraguay. A series of specimens examined in this study closely match van der Weele's description, and appear to represent a unique species. However, all of these specimens are also from southeastern Brazil, and none are from Santa Cruz Bolivia, the type locality of *chlorops* (not Vera Cruz, as stated by van der Weele 1909).

Van der Weele's *chlorops* concept seems to conflict slightly with that of Blanchard. Blanchard states that spots or stripes on the thorax are obscure. But in van der Weele's description, the pleuron of both females and males is variegated, having spotted patterns. The other features mentioned by Blanchard apply to most species of *Amoea* and do not conflict with van der Weele's description.

Three species examined in this study have been recorded from in or near Santa Cruz, Bolivia: *Amoea arenosa*, *A. nivea*, and *A. periculosa*. Both *A. arenosa* and *A. periculosa* have attributes that directly conflict with Blanchard's concept: *arenosa* has distinct pale notal stripes, and *A. periculosa* has a broad yellow subalar stripe that stands out from the remainder of the pleuron. One would presume these distinctive features would have been observed and mentioned by Blanchard. Navás's *nivea*, on the other hand, has no features that conflict with the original description of *chlorops*. The pleuron is evenly pale yellow and the notum evenly brown, and both regions lack stripes or spots. However, the female is essentially unknown. A single female from Rondônia, Brazil was determined in this study to probably belong to *A. nivea*; its thoracic pleuron appears to be predominantly dark brown with an anterodorsal yellowish maculation, but the sclerites are strongly obscured with oily residue and the exact pattern is difficult to make out.

It may very well be that Blanchard's *chlorops* female is conspecific with Navás's *nivea* male. In such case *chlorops* is the older name and would take priority. However, the type specimen of *chlorops* appears to be lost, and cannot be used to confirm Blanchard's concept. It was not discovered during a recent visit to the Paris Museum, and was also missing when van der Weele (1909) performed his investigation. And the single female tentatively placed with *nivea* is in such poor condition that relying on it alone to establish an association between the two species seems premature and unwise.

In determining concepts for these species, a conservative approach that maintains nomenclatural stability in light of the presently limited taxonomic information is to follow van der Weele's concept of *chlorops* and let the name stand for the species occurring in southwest Brazil, and to overlook the Bolivian type locality until more specimens can be collected. Ideally, to reinforce this objective and anchor the taxonomic concept, a neotype for *chlorops* would be selected, but the Code requires that a neotype "come as nearly as practicable from the original type locality" (Art. 75.3.6). The closest specimen examined in this study is from Santa Catarina Brazil, nearly 1500 km away; van der Weele's Paraguay specimen is from almost 1000 km away. Thus erecting a neotype does not seem an appropriate option.

Van der Weele (1909) indicated that his *chlorops* specimens were very similar to those of *immaculata*, and suggested that the two species might be conspecific. As with *microcerus* and *albistigma*, he felt he could not synonymize the two due to a lack of specimens. Unfortunately, a similar situation still holds true. Few specimens of *chlorops* or *immaculata* were available for this study, and they do express many similar features. Further, the geographic range of *chlorops* as described here overlaps that of the few known localities for *immaculata* (based on the few specimens having fine-grained enough label data to generate a map point). However, the two species do seem to differ anatomically on several accounts (see “Discussion” for *immaculata* below).

Green eyes do not seem to be a constant feature of *chlorops* and likely were an artifact caused by the medium into which the type specimen was collected, or aging in ambient environmental conditions.

Amoea flavitaenia *new species*

(A3 Figs. 8, 81)

Etymology and nomenclatural notes.—*flavitaenia*: flavus (Latin), ‘yellow’ + taenia (Latin), ‘ribbon, fillet’, = ‘yellow stripe’. This species is named for the broad and distinct yellow subalar stripe of males and females.

Diagnosis.—Subalar stripe present, well-developed, pale to yellow; subalar stripe setae not conspicuously differentiated from that on remainder of pleuron; remainder of thoracic pleuron strongly variegated, brown colors rather subdued, earthy, yellows pale to moderately intense; pteronotal parasagittal stripes absent; deltus brown, often anteriorly opaque, but not dark. Males: pruinescent; abdomen tergum and pleuron bearing sparse coat of short whitish or pale yellow wispy setae.

Autapomorphies.—pleural membrane setae of segments 1–6 with a dense coat of medium short wispy medium brown setae, this transitioning on segments 6–8 to a somewhat dense coat of short slender black setae.

Distribution.—Costa Rica; eastern Mexico; Panama; U.S.: Louisiana.

Description.—

Size (mm). Male: length of body 31–32, abdomen 21–23, forewing 29, hind wing 24–25, antennae 18. Female: length of body 30–32, abdomen 20–21, forewing 36–40, hind wing 32–35, antennae 20–23.

Head. Breadth more or less coequal to that of mesothorax. Occiput dark reddish-brown, lateral margin with a medium sized subtriangular yellow macula, a second smaller, irregular yellow macula positioned immediately dorsad. Vertex sandy reddish-brown; plates yellowish or reddish to dark brown; setae rather dense near antennae, mixed golden yellow and dark brown anteriorly and dorsally, transitioning to pale yellow posteriorly. Extra-torular sclerites dusky to dark brown. Paraocular band dark reddish-brown adjacent to antennae, narrowly and diffusely brownish adjacent to frons and clypeus, transitioning to very pale yellow laterad. Frons dusky orange; setae dense, golden yellow, apices dark brown. Clypeus yellow, with irregular, diffuse reddish-brown maculations laterally. Labrum concolorous with mesal portion of clypeus. Mandibles bases dusky dark yellow, transitioning to very dark reddish-brown apically. Labium pale yellow, slightly paler than labrum, with a thin dark brown sagittal line. Eyes slightly larger in ventral half. Antennae flagellomere internodes dull pale to dark reddish-brown, nodes dark brown; clubs medium to dark brown, occasionally with a very diffuse yellow stripe on anterior face.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, white setae. Cervical sclerite evenly dark brown. *Pronotum.* Posterior flange posteror margin barely covering mesoacrotergite. Pronotum coloration more or less evenly dark brown, posterior flange base color dark brown, sublaterally yellowish-orange, posterior margin broadly dark brown, a variably broad dark brown sagittal stripe present. All surfaces with medium to somewhat long, slender, golden brown setae, these whiter in pruinescent males. *Pteronotum*. Base color earthy brown with pattern rather variable, mesoprescutum with a diffuse orange macula on lateral surface of anterolateral swelling and sagittal sulcus thinly yellow, lateral hemispheres of mesoscutum sometimes pale brown or yellowish, very diffuse maculations on anterolateral and mesal faces of transverse posterior swelling of mesoscutellum; velvety spots of metascutum cinnamon colored to dark brown; in females, entire surface covered with intermediately dense, medium length, fine, golden brown setae, non-pruinescent male as in female, pruinescent male with setae pale yellow to white and lateral and posterior surfaces with setae becoming denser, in both males posterior margin of meso- and metascutellum with a loose fringe of medium length, slender, pale golden yellow setae. *Pleuron* with a broad, yolk yellow subalar stripe, ventral margin of stripe rather well defined, remainder of pleuron somewhat variably variegated but predominately brown; surfaces with more or less even coat of moderately dense, very fine, pale yellow to white setae, these becoming denser, slightly longer, and white along subalar stripe.

Legs. Femora and tibiae color patterning somewhat variable, ranging from completely dark dusky yellowish brown, to ventral surfaces being yellow, with other surfaces dark dusky brown and fascia yellow. Tarsi color variable, ranging from pale reddish to very dark brown, tibial spurs only very weakly curved, almost straight, posterior spur longer than anterior one and not extending past apex of third tarsomere on pro- and mesothoracic tibiae, second tarsomere on metathoracic tibia, tibial spurs and tarsal claws dark reddish-brown. Coxae with intermediately dense, medium length, slender, very pale yellow or white setae; antennal comb setae predominately golden.

Wings. Dimension and shape. Intermediately broad, apices rounded. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal in proximal half, cells becoming narrower in distal half. Pterostigma with four to five forked and unforked brown to dark brown veinlets; membrane translucent to opaque, colorless to cream, often with a hint of brown color; veins often slightly thickened and appearing thinly margined. Deltus translucent to slightly opaque, evenly brown. Presectoral area with eight cells. Rs with five to seven forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine irregular but more or less complete rows of cells. Cubital triangle distal domain with one to three, usually two, cells . Anal area cell row with cells undivided by crossveins. *Color and patterning.* Venation brown to dark brown. Membranes of wing in females completely lacking pigment, in at least one male membranes with a slight brownish tinge, this darker in costal area. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with two to three cells, somewhat elongate and narrowed in males. Pre-Cup axillary disk pale to dark brown, slightly paler anterolaterally. Pre-Mp_1 area margin expanded in females and males, but slightly greater in males. Anal area with two rows of undivided cells.

Abdomen. In males reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. In males, more or less evenly dull dark brown, in females, dull reddish-brown, sometimes a pair of very diffuse, dark brown parasagittal spots positioned on antecostal scars and immediately anterad of posterior margin of T3 to T7; in females T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, pale yellow setae, remainder of tergum devoid of long setae, in males, T1 to proximal portion of T3 with somewhat dense, intermediately long, wispy, yellow setae, these becoming rather short and golden brown on T3 and continuing nearly to apex of abdomen. *Sternum*. Base color dark brown, ventral surfaces often nearly completely yellow, but pigment patchy and/or mottled; surfaces mostly devoid of long setae, some intermediately long, wispy, pale golden brown setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3, setae longer and denser in males. *Pleural membrane*. In females, mostly devoid of long setae; in males, membranes of segment 2 to ca. segment 5 or 6 with a dense coat of short, slender, pale yellow to golden brown setae.

Male terminalia. Unmacerated specimens. GPC and pulvini with apices very slightly visible, ectroprocts and S9 dark brown, distal margins yellow. *Macerated specimens.* S9 apical margin obtusely angled. Pulvini somewhat small, slightly less than half the length of GPC, two times as long as width at base, slightly sclerotized, bearing numerous somewhat long, somewhat slender, brown setae, a few at apex slightly more robust. GPC weakly sclerotized; in lateral view dorsally more or less entire, dorsal notch present but very small, ventrally somewhat irregular, dorsal and ventral margins slightly convergent apicad, in ventral view intermediately broad laterally. Parameres sclerotized, in lateral view unproduced, in ventral view simple, narrowly triangular, breadth at base about one-third of length, apicolateral margin irregular, proximal margins somewhat well differentiated. Pelta weakly sclerotized, very narrowly almond-shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae reddish-brown, distivalvae with apices orangish, ectoprocts dark brown and orangish. *Macerated specimens.* Ventrovalvae elongate and somewhat narrow, subtriangular, length ca. two and a half to three times width. Distivalvae in lateral view subtriangular. Linguella very weakly produced and sclerotized, bearing several short, slender, stiff, setae. Interdental space subtriangular, glabrous. Interdens sclerotized, nipple-like, apex with or without a few very short slender setae.

Variation. In specimen JRJ_00179 (A3 Fig. 8), flagellum becoming paler and yellowish in distal one-third. Specimen JRJ_00178 with pronotum posterior flange almost entirely pale yellow and small portions of other sclerites with more pale yellow maculations than in other species. Specimen JRJ_00177 with lateral portion of lateral hemisphere of mesoscutum almost completely pale orangish, anterior surface of scutellum sublaterally orangish, and mesopostnotum sublaterally yellowish-orange. Specimen JRJ_00175 with lateral faces of metascutum sharply offset and orangish. Tarsi of specimens from Mexico and Louisiana are pale to medium reddish brown; tarsi of specimens from Costa Rica and Panama are dark reddish brown to almost black.

Type material examined.—*Holotype*, female, Mexico, in FSCA collection: “MEXICO: STATE OF VERACRUZ, FORTÍN DE LAS FLORES, SUMIDERO /// PLANTA DE LA CERVECERIA, ING. DANIEL RABAGO RES. ELEV. 2500-3000 FT. /// H. V. WEEMS, JR. COLL. 21-V-1965 MALAISE TRAP /// HOLOTYPE Amoea flavitaenia Jones ♀ design. J. R. Jones 2014 /// JRJ_00175”. Condition: excellent; antennae and wings spread, no parts missing, right HW tip slightly torn.

Additional material examined.—*Costa Rica*: Alajeula (CAS: 1 ♀, JRJ_00177). *Mexico*: Veracruz (SDMC: 1 ♀, JRJ_00176). *Panama*: Panama (CAS: 1 ♂, JRJ_00178); Veraguas (CAS: 1 ♂, JRJ_00179 [A3 Fig. 8]). *USA*: Louisiana (TAMU: 1 ♀, JRJ_00174).

Morphology, biology and ecology.—Specimens were collected at elevations of 600 to 100 m. The holotype was collected on “planta cerveceria” (hops? barley?).

Discussion.—This species is very similar to the new species *periculosa* from the northern Amazon, but has more subdued body coloration and pruinescent males, and the two species seem to be separated from one another geographically. Loan specimens were identified as *vacua* and *immaculata* by various workers, but *flavitaenia* clearly differs from them. Both *vacua* and *immaculata* lack the well-defined subalar stripe, and *immaculata* occurs in southeastern Brazil, far from the range of *flavitaenia*. Only *periculosa*, *arenosa* and *impediens* also express a well-developed subalar stripe in males and females; *arenosa* and *impediens* can be easily separated by their complete pale parasagittal stripes on the pteronotum.

The U.S. specimen was collected in New Orleans and was likely incidental, perhaps blown in from a tropical storm. The nearest collection locality for other specimens in loan material is an individual taken in Veracruz, Mexico, nearly 1400 air km away.

Amoea immaculata *(Olivier, 1790)*

(A3 Figs. 9–12, 82)

Ascalaphus immaculatus Olivier, 1790

—Olivier 1790: r#5006: 246 {OD: sex not indicated [♂ (see van der Weele 1904)], D. TS: not indicated [holotype (see van der Weele 1904)]. TL: “l’Amérique méridionale” [South America]. TR: “collection de M. Gigot d’Orcy” [RMNH:

see van der Weele 1904]. Type specimen not examined (see “Discussion” below).}

—McLachlan 1871.09.14 r#353: 238 {SYN}

—van der Weele 1904 r#397: 204 {DIS, SYN, TR, TS}

—van der Weele 1909.01.05 r#420: 34 {SYN}

—Navás 1911 r#535: 23 {DIS}

—Navás 1930 r#882: 127 {DIS}

—Orfila 1949 r#5020: 190 {SYN}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: SYN}

—Penny 1978.09.15 r#5098: 11 {SYN}

—Oswald and Penny 1991.12.02 r#7138: 8 {SYN}

Haploglenius immaculatus (Olivier, 1790)

—McLachlan 1871.09.14 r#353: 238 {BIO, DIS, NC, TL}

—van der Weele 1904 r#397: 204 {SYN}

—van der Weele 1909.01.05 r#420: 34 {SYN}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: SYN}

—Penny 1978.09.15 r#5098: 11 {SYN}

Amoea immaculata (Olivier, 1790)

—van der Weele 1909.01.05 r#420: 34, fig. 9 {DIS, GD, NC, RD: ♂♀, SYN, TR, TS}

—Navás 1912b.10.31 r#542: 210 {D, GD, K}

—Navás 1913 r#1207: 49 {D, GD, K}

—Navás 1930 r#882: 127 {DIS}

—Shetlar 1977 r#5727: 79, figs. 15a-b, 21, 36 {Ph.D. dissertation, nomenclatural acts invalid: D, DIS, GD, RD: ♂♀, SYN, TR ["University of Berlin, Zoology Museum". MFNB? See "Discussion below"], TS}

—Penny 1978.09.15 r#5098: 11 {GD, L, SYN}

—Penny 1982a r#5105: 395 {MOR, SYN}

—Penny 1982b r#5103: 616 {SYN}

Ascalaphus subcostatus Burmeister, 1839

—Burmeister 1839 r#1771: 1000 {OD: ♂. TS: syntypes: ♂♂ [a lectotype needs to be designated from syntype material]. TL: Brazil. TR: "v. Winthems Sammlung" (MCZ—see van der Weele 1909). Type specimen not examined (see "Discussion" below).}

—Lefèbvre 1842.04.?? r#3666: 6 {L (under new genus *Amoea*)}

—Hagen 1861.07.?? r#455: 327 {GD, L, SYN}

—Hagen 1866 r#460: 379, 387 {L, SYN}

—McLachlan 1871.09.14 r#353: 236 {SYN}

—van der Weele 1909.01.05 r#420: 34 {DIS, JSYN (of *Ascalaphus immaculatus* Olivier)}

—Orfila 1949 r#5020: 189 {DIS, JSYN (of *Ascalaphus immaculatus* Olivier)}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Ascalaphus immaculatus* Olivier)}

—Oswald and Penny 1991.12.02 r#7138: 8 {JSYN (of *Ascalaphus immaculatus* Olivier), TSP (of *Amoea* Lefèbvre, following Penny 1982a)}

Amoea subcostata (Burmeister, 1839)

—Lefèbvre 1842.04.?? r#3666: 6 {NC}

—Hagen 1866 r#460: 379, 387 {L, SYN}

—van der Weele 1909.01.05 r#420: 34 {JSYN (of *Ascalaphus immaculatus* Olivier}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Ascalaphus immaculatus* Olivier)}

Haploglenius subcostatus (Burmeister, 1839)

—Hagen 1866 r#460: 379, 387, 406 {GD, NC, SYN}

—McLachlan 1871.09.14 r#353: 236 {DIS, GD, L, TS}

—van der Weele 1909.01.05 r#420: 34 {JSYN (of *Ascalaphus immaculatus* Olivier)}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1982a r#5105: 395 {JSYN (of "*Amoea immaculata* Olivier"), TSP (of *Amoea* Lefèbvre)}

Ascalaphus injurius Walker, 1853

—Walker 1853 r#6194: 447 {OD: sex not indicated [♀], D. TS: not indicated [holotype by explicit monotypy]. TL: Brazil. TR: BMNH. Type specimen examined (see "Type material examined" below).}

—Hagen 1861.07.?? r#455: 327 {JSYN (of *Ascalaphus subcostatus* Burmeister)}

—Hagen 1866 r#460: 383 {JSYN (of "*Haploglenius subcostatus* Br."), L}

—McLachlan 1871.09.14 r#353: 236 {SYN}

—van der Weele 1909.01.05 r#420: 34 {JSYN (of *Ascalaphus immaculatus* Olivier)}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Ascalaphus immaculatus* Olivier)}

Haploglenius injurius (Walker, 1853)

—McLachlan 1871.09.14 r#353: 236 {GD, NC, RD: ♀, SYN}

—van der Weele 1909.01.05 r#420: 34 {JSYN (of *Ascalaphus immaculatus* Olivier)}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Ascalaphus immaculatus* Olivier)}

Ascalaphus damnosus Walker, 1853 **new synonym**

—Walker 1853 r#6194: 449 {OD: sex not indicated [♂, not ♀ as indicated in van der Weele 1904], D. TS: not indicated [holotype by explicit monotypy]. TL: indicated as unknown. TR: BMNH. Type specimen examined (see "Type material examined" below).}

—Hagen 1861.07.?? r#455: 327 {JSYN (of *Ascalaphus subcostatus* Burmeister)}

—Hagen 1866 r#460: 382 {JSYN (of "*Haploglenius subcostatus* Br."), L}

—McLachlan 1871.09.14 r#353: 236 {SYN}

—van der Weele 1904 r#397: 204 {DIS, TS}

—van der Weele 1909.01.05 r#420: 35 {JSYN (of *Ascalaphus chlorops* Blanchard)}

—Williner 1945 r#6292: 427 {JSYN (of *Ascalaphus chlorops* Blanchard)}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Ascalaphus chlorops* Blanchard)}

Haploglenius damnosus (Walker, 1853)

—McLachlan 1871.09.14 r#353: 236 {DIS, GD, NC, RD: ♀, SYN}

—van der Weele 1909.01.05 r#420: 35 {JSYN (of *Ascalaphus chlorops* Blanchard)}

—Williner 1945 r#6292: 427 {JSYN (of *Ascalaphus chlorops* Blanchard)}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Ascalaphus chlorops* Blanchard)}

Haploglenius dupuyi Navás, 1923 **new synonym**

—Navás 1923a r#752: 773, fig. 3 {OD: sex not indicated [♂], D. TS: not indicated [holotype by explicit monotypy]. TL: "Brasil, Rio de Janeiro". TR: MNHN. Type specimen examined (see "Type material examined" below).}

—Penny 1978.09.15 r#5098: 13 {GD, L}

—Penny 1982b r#5103: 608 {DIS}

—Ábrahám 2013.04.30 r#?????: 185 {DIS, GD, SYN, TL, TR, TS (see "Type material examined" below)}

Etymology and nomenclatural notes.—*immaculata*: immaculata (Latin), 'unspotted'. Referring to the clear wings, as opposed to the other species Olivier (1790) described in the same work, *Ascalaphus maculatus* (now *Puer maculatus*, a valid species).

Diagnosis.—Pteronotum with parasagittal stripes absent, but often appearing overall yellowish from yellow maculations, setae somewhat dense and pale yellow to white. Subalar stripe absent; pleuron strongly variegated brown and yellow, colors not subdued, predominantly yellow. Costal and subcostal areas sometimes faintly tinted. Wings larger than other species (FW: males >35 mm; females >38 mm). Males: not pruinescent; HW base expanded as in other species, but expanded area slightly broader; abdominal tergum and pleural membrane setae extremely sparse, with a very few wispy ones on T1.

Autapomorphies.—male FW subcostal area devoid of pigment; T9 dorsal surface of males with some parts of lateral marginal surfaces cream or yellow.

Distribution.—Southeastern Brazil.

Description.—

Size (mm). Male: length of body 32–35, abdomen 22–25, forewing 35–38, hind wing 32–34, antennae 21–22. Female: length of body 32, abdomen 21, forewing 39–40, hind wing 36, antennae 21.

Head. Breadth slightly superequal to that of mesothorax. Occiput pattern often obscured, more or less dark brown, mesolateral margin with a diffuse yellow triangular maculation, a smaller irregular yellow macula on lateral margin immediately posterad of posterolateral plate. Vertex sandy to dark brown; vertex plates concolorous to slightly darker than vertex; setae somewhat dense near antennae, golden with tips dark brown and some dark brown setae mixed in dorsally, transitioning to brown dorsally and pale golden posteriorly. Extra-torular sclerites dusky orange. Paraocular band dark brown laterad of antennae, transitioning to yellow adjacent to frons. Frons dark brown in dorsal one-fourth, transitioning to dusky pale yellow or orangish; setae somewhat dense, pale or golden-yellow, a few dark brown ones dorsolaterally. Clypeus pale yellow to dusky orangish. Labrum concolorous with clypeus. Mandibles concolorous with labrum basally, transitioning to very dark reddish-brown apically. Labium concolorous with mandible bases, sagittal brown line incomplete distally, very diffuse, or altogether absent. Eyes slightly larger in ventral half. Antennae flagellomere internodes yellowish to reddish brown, nodes pale yellowish-brown; clubs dark brown, often with anterior face diffusely yellowish or orange.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, pale golden setae. Cervical sclerite pale orange to dark brown. *Pronotum.* Posterior flange posteror margin not quite covering mesoacrotergite. Pronotum coloration variable, anterior flange and medial transverse band evenly pale orange or dark brown, with many small, diffuse, orange maculae, posterior flange predominately orange, often posterior margin dark brown and this contiguous with a diffuse dark brown sagittal line. All surfaces with somewhat long, slender, pale golden brown setae. *Pteronotum*. Base color dark brown, pattern sometimes obscured, but when well expressed with large diffuse orange maculations on anterior margin and lateral faces of mesoprescutum, mesotegula, lateral halves of mesoscutum, anterior face of mesoscutellum, anterolateral and mesal faces of transverse posterior swelling of mesoscutellum, and laterally and posteriorly on metascutum and metascutellum; velvety spots of metascutum orangish to dark brown; entire surface of pteronotum covered with somewhat dense, intermediately long, very fine, dull golden brown setae, setae very slightly denser, longer, and paler on posterolateral surfaces of mesoscutum, mesoscutellum, metascutum, and metascutellum.

Pleuron with color strongly variegated, yolk-yellow and dark brown with slightly more yellow than brown; all surfaces more or less evenly covered with a somewhat dense coat of intermediately long, very slender, pale yellow setae, these sometimes slightly denser and longer on mes- and metanepisternum.

Legs. Femora pale yellow in proximal third, transitioning to dusky brown in distal two-thirds, at least on anterolateral surfaces; tibiae pale to medium yellow, sometimes completely, usually anterolateral surfaces either evenly dark brown or dark brown in proximal and distal thirds with mesal third yellow, concolorous with remainder of tibia. Tarsi very dark reddish-brown, almost black, terminal tarsomere with apex diffusely pale reddish, tibial spurs only very weakly curved, almost straight, posterior spur longer than anterior one and extending approximately to apex of second tarsomere, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, very pale yellow setae; antennal comb setae golden.

Wings. Dimension and shape. Large, intermediately broad, apically rounded, subacute. *Venation/cells.* FW. Costal area with subcostal veinlets very slightly inclined, cell width and height more or less coequal in proximal half of wing, cells slightly narrower in distal half. Pterostigma with ca. four forked and unforked brown veinlets; membrane pale cream white to slightly brownish or altogether devoid of pigment, usually translucent but sometimes becoming slightly opaque; veins often thickened and very thinly margined. Deltus opaque yellowish brown, pigment anteriorly darker and denser, sometimes posteriorly slightly translucent. Presectoral area with eight cells. Rs with six forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. eight to ten irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells . Anal area cell row sometimes with one distal cell divided by a crossvein. *Color and patterning.* Venation pale to moderately dark brown, usually medium brown. Membranes of wing mostly completely lacking pigment, but costal and subcostal areas sometimes weakly tinged with brown color, particularly in males. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with two to three cells. Pre-Cup axillary disk dark brown, distally narrowly translucent to pale yellow. Pre-Mp_1 area margin broadly expanded in both males and females, expansion deeper in males. Anal area with two rows of cells.

Abdomen. In males not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly medium to dark brown, sometimes paler, orangish, with a narrow sagittal brown stripe, sometimes each tergite with a very diffuse, transverse, dark brown maculation positioned immediately anterad of posterior margin; T1 with dense, long, wispy, pale golden setae, T2 laterally with some medium length, wispy, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. Sometimes evenly dark brown, but sometimes with a pattern beginning to form, as follows. S2 to S4 laterally dark brown, mesally yolk yellow, posterior margin of S3 and S4 with brown pigment forming a broad transverse band, this bisected by a narrow sagittal line of yellow pigment, often a second, rather diffuse, transverse band of brown pigment immediately posterad of sternite midpoint, and a thin diffuse brown sagittal line on mesal portion of sternite, this pattern sometimes weakly expressed on subsequent sternites; surfaces mostly devoid of long setae, some intermediately long, wispy, pale golden setae on entire surface of S2 and proximal portions of S3. *Pleural membrane*. Devoid of long setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible. *Macerated specimens.* Not available.

Female terminalia. Apex of abdomen either missing or unable to be dissected (see "Discussion") in all available females, unable to evaluate.

Variation. In one specimen (JRJ_01625) presectoral area in right FW with ten cells (left FW with normal count of eight cells).

Type material examined.—Holotype of *Ascalaphus injurius* (A3 Fig. 12), female, Brazil, in BMNH collection: "Brazil /// injurius /// Type /// injurius WLK /// JRJ_01625". Condition: fair, wings and antennae spread, left antennae, right mesothoracic leg, right HW apex, and most of abdomen missing, all wing margins slightly tattered or torn. Holotype of *Ascalaphus damnosus* (A3 Fig. 11), male, Brazil, in BMNH collection: "Type /// 37 /// damnosus /// damnosus WLK /// JRJ_01613". Condition: poor, wings and antennae spread, left antennae, left meso- and metathoracic legs, and left FW apex missing, all wings torn, left wings especially tattered, entire body covered in a opaque white residue, obscuring features. Holotype of *Haploglenius dupuyi*, male, Brazil, in MNHN collection: "MUSEUM PARIS BRÉSIL RIO-JANEIRO Dr DUPUY 1910 /// TYPE /// Haploglenius Dupuyi Nav. P. Navás S. J. det. ///JRJ_01224"; condition: very poor, thorax crushed and parts glued back together, legs, right wingtips and most of left HW missing, wing margins very tattered.

Additional material examined.—*Brazil*: Rio de Janeiro (MNHN: 1 ♂, JRJ_01615); locality unknown (MFNB: 1 ♂, JRJ_01704 [A3 Fig. 9], 1 ♀, "zaborabas" specimen [see van der Weele 1909: 35] JRJ_01729 [A3 Fig. 10]).

Morphology, biology and ecology.—The few known specimens of *immaculata*, including the various types examined in this study, appear to have been collected in the southeastern coastal forests of Brazil (Rio de Janeiro and environs) in the mid 1800's and early 1900's. These areas were among the first regions of Brazil to be colonized and developed by early settlers, and it makes sense that early collections records would come from there. Much of the original forest is now gone or reduced to relatively small preserves (M. Machado, pers. comm..), and it is not certain if *immaculata* can still be found there today.

Discussion.—Although the specimens available for this study were in rather poor condition, it was possible to interpret, code and analyze characters from them for the cladistic analysis, and *immaculata* was placed as the most basal species in the genus. One of the most conspicuous features of the species is its larger size relative to other described species. Van der Weele (1909) considered *immaculata* to be a transition species from *Episperches* (now part of *Amoea*) to *Byas* (now *Ascalobyas*), partially on the basis of its size and wing shape, and his assessment appears to be borne out in the phylogeny.

Van der Weele (1904, 1909) was able to examine Olivier's type in the Leiden Museum, and found it to agree with a specimen labeled with the word "Zaborabas". The *Zaborabas* specimen (JRJ_01729) was also available for this study, and, though deteriorated, in several regards it is in better condition than any of the types. For example, although its abdomen has been glued on upside down, it is the only female in all available material possessing a complete abdomen apex; it might have been a prime candidate for dissection were not an inserted stout metal pin preventing such action. Shetlar (1977) gave the "University of Berlin, Zoology Museum" (MFNB?) as the type repository for Olivier's type, but this disagrees with van der Weele (1904, 1909), and the type specimen was not found in material borrowed from the MFNB. A male borrowed from the MFNB is the specimen photographed by van der Weele (1909: 34, fig. 9), but van der Weele did not indicate this to be the type.

Van der Weele (1909) made *Ascalaphus subcostatus* a synonym of *immaculata* after examining a photograph of one of the syntypes, which he referred to as the type male. He considered *injurius* to be a synonym of *immaculata*. Although the type female is missing wingtips and an abdomen, its head and thorax lack the obscuring residues found on other specimens, and the predominately yellow-orange patterns of the species can be more clearly seen. It agrees rather well with the *Zaborabas* specimen in wing size and shape and in patterns of the body. Van der Weele placed *damnosus* as a synonym of *chlorops*, but its large size with the HW pre-Mp_1 area broadly expanded and the darkened costal areas indicate it belongs with *immaculata*; it agrees well with the *injurius* type, for example in thorax patterning, but differs in its male-specific features (e.g., costal area darkening). Penny (1982b) considered *dupuyi* to be a species of *Ascalobyas*, but its variegated thoracic pleuron, antennal length, and wing patterning all place it with *immaculata*. McLachlan (1871) discussed *subcostatus* and the genus *Haploglenius*, and postulated that Burmeister (1839) could not have been looking at males because he didn't mention the prothoracic valve, but McLachlan did not understand that the valve is absent in *subcostatus* and congeners, which are now understood to belong to *Amoea*.

As discussed earlier, *immaculata* agrees highly but not completely with *chlorops*. In *immaculata* the wings are larger (male FW > 35 mm; female FW > 38mm), the pleuron with more yellow maculation, males have the costal areas more readily lightly fuscous and the pre-Mp_1 area margin more deeply expanded, the tibia anterolateral surface is dark brown in the proximal and distal third while the mesal third is concolorous with the remainder of tibia, and the FW deltus is opaque yellowish brown with the pigment anteriorly darker and denser. In *chlorops*, the wings are smaller (male FW < 34 mm; female FW < 37 mm), the thorax with predominately dark earthy brown with smaller yellow maculations, the costal areas are rarely only very weakly fuscous, the tibia anterolateral surfaces are evenly dark brown, and the deltus is translucent brown, becoming dark anteriorly.

Amoea impediens *(Walker, 1853)*

(A3 Figs. 13–14, 79)

Ascalaphus impediens Walker, 1853

—Walker 1853 r#6194: 449 {OD: ♂♀], D. TS: not indicated [syntypes: 1 ♂, 1♀; a lectotype needs to be designated from syntype material]. TL: "Pará (Brazil); "Santarem" (Brazil). TR: BMNH. Female syntype specimen examined (see "Type material examined" below).}

—Hagen 1861.07.?? r#455: 327 {JSYN (of *Ascalaphus subcostatus* Burmeister)}

—Hagen 1866 r#460: 383 {L, SYN}

—McLachlan 1871.09.14 r#353: 238 {SYN}

—van der Weele 1906 r#404: 227 {SYN}

—van der Weele 1909.01.05 r#420: 42 {SYN}

—Penny 1978.09.15 r#5098: 12 {SYN}

—Penny 1982b r#5103: 616 {JSYN (of *Ascalaphus iniquus* Walker), MOR, TR}

Haploglenius impediens (Walker, 1853)

—McLachlan 1871.09.14 r#353: 237, 238 {DIS, GD, MOR, NC, RD: sex not indicated, SYN}

—van der Weele 1909.01.05 r#420: 42 {SYN}

—Penny 1978.09.15 r#5098: 12 {SYN}

—Penny 1982b r#5103: 616 {JSYN (of *Ascalaphus iniquus* Walker)}

Episperches impediens (Walker, 1853)

—van der Weele 1909.01.05 r#420: 42, fig. 15 {GD, NC, RD: ♂♀, SR, SYN, TL}

—Navás 1912b.10.31 r#542: 211 {D, GD, K}

—Navás 1913 r#1207: 51 {D, GD, K}

—Penny 1978.09.15 r#5098: 12 {GD, L, SYN}

—Penny 1982a r#5105: 395 {MOR}

—Penny 1982b r#5103: 616 {JSYN (of *Ascalaphus iniquus* Walker)}

Episperches taeniatus Gerstaecker, 1894

—Gerstaecker 1894 r#2559: 99 {OD: ♂, D. TS: not indicated [holotype by monotypy—see van der Weele 1909]. TL: "Iquitos" (Peru). TR: not indicated [EMAU—see Penny 1982b]. Type specimen not examined (see "Discussion" below).}

—van der Weele 1906 r#404: 227 {JSYN (of *Ascalaphus impediens* Walker)}

—van der Weele 1909.01.05 r#420: 42 {JSYN (of *Ascalaphus impediens* Walker)}

—Penny 1978.09.15 r#5098: 12 {JSYN (of *Ascalaphus impediens* Walker)}

—Penny 1982b r#5103: 616 {JSYN (of *Ascalaphus impediens* Walker), TR}

Etymology and nomenclatural notes.—*impediens*: impedio (Latin), 'hinder, prevent, obstruct'. The reason for the selection of this name is not provided in the original description.

Diagnosis.—Notal parasagittal stripes present, usually narrow and well-defined. Subalar stripe present, well-developed, yellow; subalar stripe setae dense, long and silky white, longer than on remainder of pleuron; venter of subalar stripe bordered by ventrally well defined broad brown stripe. Males: not pruinescent; HW axillary cord setae white, thick.

Autapomorphies.—pleural stripe subtending subalar stripe present, broad, well defined, brown; subalar setae undifferentiated from that on remainder of pleuron.

Distribution.—Brazil; Peru.

Description.—

Size (mm). Male: length of body 29–32, abdomen 19–22, forewing 27–30, hind wing 23–25, antennae 17–20. Female: length of body 27–29, abdomen 17–19, forewing 32–34, hind wing 29–30, antennae 19–20.

Head. Breadth more or less coequal to that of mesothorax. Occiput with an irregular pattern of dark brown and yellow maculations. Vertex sandy to brown; plates dark brown; setae rather dense near antennae, mixed golden yellow and dark brown anteriorly and dorsally, transitioning to pale golden yellow posteriorly. Extra-torular sclerites dull dark reddish- or orangish-brown. Paraocular band dull dark yellowish, possibly bright yellow in life. Frons bright dusky orange; setae dense, concolorous with that on anterior portion of frons. Clypeus yellow to dusky orangish-brown, some diffuse reddish-brown maculations often present laterally. Labrum concolorous with mesal portion of clypeus. Mandibles bases concolorous with labrum, transitioning to very dark reddish-brown apically. Labium pale yellow, slightly paler than mandible base and labrum, with a thin dark brown sagittal line. Eyes slightly larger in ventral half. Antennae flagellomere internodes yellowish to reddish brown, nodes dark reddish brown, nodes of three to five flagellomeres proximad of club with a few very short apical setae; clubs medium to dark brown, often with a diffuse broad yellow stripe on anterior face.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, pale yellow setae. Cervical sclerite evenly dark brown. *Pronotum.* Posterior flange posteror margin barely covering mesoacrotergite. Pronotum coloration more or less evenly dark brown, posterior flange mesally yellow or orangish, with posterior margin sublaterally yellowish, mesal margin broadly dark brown, and a variably broad dark brown sagittal stripe present. All surfaces with medium to somewhat long, slender, golden brown setae. *Pteronotum*. Base color dark brown with narrow, sublateral, rarely diffuse, orangish-yellow to pale brown stripes running longitudinally from anterolateral surface of mesoprescutum to posterolateral surface of metascutellum, metaprescutum and scutum usually evenly dark brown; velvety spots of metascutum dark brown, darker than other surfaces of sclerite; entire surface of mesonotum covered with intermediately dense, somewhat short, slender, golden brown setae, this becoming denser and longer on posterolateral surface of scutum, posterior margin of metascutellum with a dense fringe of medium length, slender, white setae, dorsal and posterolateral surfaces of metascutum and scutellum with a dense coat of medium long, slender, white setae. *Pleuron* with yellow color aggregated along sclerites subtending wing bases and forming a broad yolk yellow subalar stripe, surfaces subtending stripe with color also aggregated, this into a broad brown stripe, ventral margin of brown stripe well defined, surfaces ventrad of it more or less orangish-yellow, meso- and metakatepimeron mostly dark brown, yellow subalar stripe bearing a dense coat of moderately long, slender, silky, white setae, remaining surfaces bearing a moderately dense coat of intermediately long, very slender, golden brown setae.

Legs. Femora and tibiae more or less orangish-yellow proximoventrally, dorsal and lateral surfaces somewhat dusky brown to dark brown. Tarsi dark reddish-brown, tibial spurs only very weakly curved, almost straight, not extending past apex of third tarsomere on pro- and mesothoracic tibiae, second tarsomere on metathoracic tibia, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, white setae; antennal comb setae predominately golden, black distally.

Wings. Dimension and shape. Intermediately broad, apically very subtly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal. Pterostigma with four to six forked and unforked brown veinlets; membrane pale brown, sometimes with a tinge of cream color, usually translucent but sometimes becoming slightly opaque; veins often slightly thickened and appearing very thinly margined. Deltus usually completely lacking pigment, sometimes translucent yellowish, rarely posteromesally tinged with brown. Presectoral area with eight cells. Rs with six forks. Mp_2 + Cua_1 evenly curving toward hind margin in distal portion. Cubital area with ca. seven to nine irregular but more or less complete rows of cells. Cubital triangle distal domain with one to three, usually two, cells . Anal area cell row with cells undivided by crossveins. *Color and patterning.* Venation pale to moderately dark brown, usually medium brown. Membranes of wing completely lacking pigment. HW. As in forewing except as follows. Mp_2 fork angle nearly 90°. Medial triangle distal domain with two to three cells, slightly elongate and narrowed in males. Pre-Cup axillary disk brown to dark brown, distal margin devoid of pigment to slightly whitish or yellowish. Pre-Mp_1 area margin expanded, more so in males. Anal area with two rows of undivided cells.

Abdomen. In males reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Base color dull dark brown, vestiges of a pair of broad pale yellow to orangish parasagittal stripes sometimes expressed along full length and separated by a narrow dark brown sagittal line, pale stripes sometimes with numerous small dark flecks, a pair of small, diffuse, very dark brown parasagittal spots positioned immediately anterad of posterior margin of T4 to T8; In females, T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, pale golden setae, remainder of tergum devoid of long setae, in males, T1 with a dense covering of long, slender, white setae, T2 to proximal portion of T4 with a dense covering of very short, slender, wispy, whitish to pale yellow setae. *Sternum*. Base color dark brown, S1 proximal membrane and anteromesal portion of S2 predominately diffusely yellow, a medium large, round diffuse yellow macula on anterior portion of S3, mesoventral surfaces of S3 to S7 often becoming largely yellow; surfaces mostly devoid of long setae, some intermediately long, wispy, pale gold setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3. *Pleural membrane*. In females, mostly devoid of long setae; in males, membrane of segment 2 with long, wispy, white setae dorsally, golden ventrally, membrane of segments 3 and 4 with a dense coat of short, wispy, orangish to golden yellow setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible. *Macerated specimens.* S9 apical margin obtusely angled. Pulvini moderately small but well developed, apically sclerotized, two to three times as long as width at base, bearing numerous intermediately long, slender, brown setae. GPC somewhat sclerotized basally; in lateral view dorsally more or less entire, dorsal notch present but shallow, ventrally more or less entire, dorsal and ventral margins slightly convergent apicad; in ventral view intermediately broad laterally. Parameres sclerotized, in lateral view unproduced, in ventral view simple, slightly elongate, appearing like cloven hooves of a deer, but not curved, proximal margins weakly differentiated. Pelta weakly sclerotized, very narrowly almond-shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distivalvae and ectoprocts dark brown. *Macerated specimens.* Not available.

Variation. A single specimen from Peru with pteronotal stripes slightly broader and diffuse (JRJ_00201).

Type material examined.—Syntype, female, Brazil, in BMNH collection: "Type /// Para /// impediens /// impediens Wlk /// JRJ_01627". Condition: good, wings and antennae spread, right FW broken and reattached with glue, left antennae apex and FW tip missing.

Additional material examined.—*Brazil*: Para (CMNH: 5 ♂♂, JRJ_00195, JRJ_00196, JRJ_00197 [A3 Fig. 13], JRJ_00198, JRJ_00199, 1 ♀, JRJ_00200 [A3 Fig. 14]); locality unknown (BMNH: 1 ♂, JRJ_01619). *Peru*: Madre de Dios (CAS: 1 ♂, JRJ_00201). *Country unknown*: (BMNH: 1 ♂, JRJ_01618).

Morphology, biology and ecology.—Nothing is known about the biology or specialized morphology of this species.

Discussion.—This attractive species is very similar to *arenosa*—both display pale parasagittal stripes on the pteronotum—but it can be easilydiagnosed by the white setae on the subalar stripe being very thick and silky and in having both the subalar stripe and the broad brown stripe subtending the subalar stripe well-defined. The pteronotal stripes of *impediens* are also usually narrower and more well-defined than in *arenosa*.

Gerstaecker's (1894) original description of *taeniatus* agrees very slowly with *arenosa* (presence of pteronotal stripes, the pleuron predominately pale yellow with a 'blackish longitudinal bruise', pleural setae with a 'satin finish').

Amoea iniqua ***(Walker, 1853)***

(A3 Figs. 15–16, 82)

Ascalaphus iniquus Walker, 1853

—Walker 1853 r#6194: 448 {OD: sex not indicated [♂], D. TS: not indicated [holotype by explicit monotypy]. TL: Brazil. TR: BMNH. Type specimen examined (see “Type material examined” below).}

—Hagen 1861.07.?? r#455: 327 {GD, L, SYN}

—Hagen 1866 r#460: 383 {L, SYN}

—McLachlan 1871.09.14 r#353: 237 {SYN}

—van der Weele 1909.01.05 r#420: 39 {SYN}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 12 {SYN}

—Penny 1982b r#5103: 616, 619 {SYN, MOR, TR}

—Oswald and Penny 1991.12.02 r#7138: 8 {TSP (of *Episperches* Gerstaecker, following Navas1912c)

Haploglenius iniquus (Walker, 1853)

—Hagen 1866 r#460: 406 {GD, L, NC}

—McLachlan 1871.09.14 r#353: 237 {GD, RD: ♀, SYN}

—van der Weele 1909.01.05 r#420: 39 {SYN}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus*)}

—Penny 1978.09.15 r#5098: 12 {SYN}

—Penny 1982b r#5103: 616 {SYN}

Episperches iniquus (Walker, 1853)

—van der Weele 1909.01.05 r#420: tafel I, 39, fig. 4 {D, DIS, GD, NC, RD: ♂♀, SYN, TR, TS}

—Navás 1912b.10.31 r#542: 211 {D, GD, K}

—Navás 1913 r#1207: 50 {D, GD, K}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus*)}

—Penny 1978.09.15 r#5098: 12 {GD, L, SYN}

—Penny 1982b r#5103: 616 {SYN}

Amoea iniqua (Walker, 1853)

—Penny 1982b r#5103: 616, fig. 6, map 4 {FP, GD, H, NC, RD: ♂♀, SR, SYN, TR, TS}

Episperches irideus Gerstaecker, 1894

—Gerstaecker 1894 r#2559: 99 {OD: ♂, D. TS: not indicated [syntypes: 2 ♂♂—see van der Weele 1909; a lectotype needs to be designated from syntype material]. TL: “Itaituba (Alto-Amazonas)” (Brazil). TR: not indicated [EMAU—see Penny 1982b]. Type specimen not examined (see “Discussion” below).}

—van der Weele 1906 r#404: 227 {JSYN (of *Ascalaphus iniquus* Walker)}

—van der Weele 1909.01.05 r#420: 39 {DIS, JSYN (of *Ascalaphus iniquus* Walker), TL}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus*)}

—Penny 1978.09.15 r#5098: 12 {JSYN (of *Ascalaphus iniquus* Walker)}

—Penny 1982b r#5103: 616 {JSYN (of *Ascalaphus iniquus* Walker)}

Etymology and nomenclatural notes.—*iniqua*: iniquus (Latin), ‘uneven, unjust, hurtful’. The significance of this name and the reason for its selection by Walker are not indicated in the original description and are unclear.

Diagnosis.—Pteronotal parasagittal stripes absent; notum evenly dark golden or honey brown, yellow maculations indistinct. Subalar stripe absent, or very weakly hinted at and broad; pleuron otherwise variegated yellow and brown but subdued, usually appearing yellowish or orangish overall with some brown markings (males), sometimes darker brownish overall with yellow markings (females). Males: pre-Mp_1 area margin narrow and posteriorly more expanded than in other species, marginal cell row of the anal area with a few to several cells in distal half divided by crossveins, thorax not pruinescent;

abdominal tergum and pleural membrane setae extremely sparse, with a very few wispy ones on T1.

Autapomorphies.—male pronotum flange dorsally evenly medium brown; pulvini very small and poorly developed, apex with small apical tuft of intermediately long setae.

Distribution.—Brazil; French Guiana.

Description.—

Size (mm). Male: length of body 25–36, abdomen 15–24, forewing 31–33, hind wing 25–26, antennae 19–21. Female: length of body 22–31, abdomen 15–20, forewing 34–36, hind wing 29–31, antennae 18–19.

Head. Breadth more or less coequal to that of mesothorax. Occiput with an irregular and often obscured pattern of dull dark brown and yellow maculations. Vertex sandy to reddish or dull yellowish brown; vertex plates dark brown to grayish-yellow; setae rather dense near antennae, golden yellow with some dark brown setae mixed in anteriorly and dorsally, transitioning to just golden yellow to dark brown posteriorly. Extra-torular sclerites dusky orange to dark brown, often concolorous with prefrons and dorsal most portions of paraocular band laterad of antennal bases. Paraocular band yellow adjacent to frons, transitioning to dark amber brown laterad of antennae. Frons medium dusky orange; setae moderately dense, mixed golden-yellow and dark brown to black. Clypeus pale to dusky yellow, laterally often with very diffuse reddish-brown maculations.

Labrum concolorous with clypeus. Mandibles concolorous with labrum basally, transitioning to very dark reddish-brown apically. Labium pale to orangish-yellow, with a thin dark brown sagittal line. Eyes slightly larger in ventral half. Antennae flagellomere internodes yellowish to reddish brown, nodes dark reddish brown, nodes of three to five flagellomeres proximad of club with a few short apical setae; clubs medium to dark brown, often with a hint of a diffuse orange stripe on anterior face.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, golden brown setae. Cervical sclerite pale to dark brown, darker apically. *Pronotum.* Posterior flange posteror margin not quite or just barely covering mesoacrotergite. Pronotum coloration more or less evenly medium to dark brown, posterior flange dark brown. All surfaces with medium to somewhat long, slender, brown setae. *Pteronotum*. More or less evenly medium brown, but sometimes dull dusky yellowish, honey orange, or dark brown, anterolateral faces of mesoprescutum narrowly diffusely yellow or orange, anterior surface of mesoscutellum sometimes with sublateral dull orangish teardrop-shaped maculae, posterior transverse swelling of mesoscutellum sometimes with very diffuse lateral and mesal dull orangish maculae; velvety spots of metascutum orangish to dark brown, sometimes darker than other surfaces of sclerite; entire surface of pteronotum covered with moderately dense, intermediately long, very fine, golden brown setae, setae somewhat denser and longer on posterolateral surfaces of mesoscutum, mesoscutellum, metascutum, and metascutellum. *Pleuron* with color variegated; in males, predominately dull yellow, sclerites subtending wing bases mostly yellow and sometimes appearing as a broad but irregular subalar stripe with an irregular ventral margin, remainder of pleuron variegated but mostly yellow; females highly variable, variegated, varying from predominately dark brown to predominately bright yellow, sometimes dull yellow and pale brown; all surfaces more or less evenly covered with a somewhat dense coat of moderately short, very slender, pale yellow setae.

Legs. Femora and tibiae ventral and posterolateral surfaces pale yellowish, evenly transitioning to dusky dark reddish-brown on dorsal and anterolateral surfaces. Tarsi reddish to dark reddish-brown, tibial spurs only very weakly curved, almost straight, not extending past apex of second tarsomere, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, very pale yellow setae; antennal comb setae predominately golden, black distally.

Wings. Dimension and shape. Intermediately broad, apically rounded, very slightly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal. Pterostigma with four to five forked and unforked brown veinlets; membrane pale brownish to cream yellow, often opaque; veins often thickened and very thinly margined. Deltus sometimes completely lacking pigment, usually translucent yellowish or pale brown. Presectoral area with eight cells. Rs with six to seven forks. Mp_2 + Cua_1 evenly curving toward hind margin in distal portion. Cubital area with ca. seven to nine irregular but more or less complete rows of cells. Cubital triangle distal domain with two cells . Anal area cell row rarely with one or two cells divided by crossveins. *Color and patterning.* Venation pale to moderately dark brown, usually medium brown. Membranes of wing completely lacking pigment. HW. As in forewing except as follows. Mp^2 fork angle nearly 90°. Medial triangle distal domain with two to three cells, longer and narrower in males. Pre-Cup axillary disk dark brownish proximally, translucent anterodistally. Pre-Mp_1 area margin slightly expanded in females, greatly expanded in males. Anal area with two rows of cells, in males, marginal row with several cells in distal half divided by crossveins.

Abdomen. In males reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Base color dull dark brown, a pair of broad cinnamon-colored to slightly reddish parasagittal stripes expressed along full length, each tergite with a small, diffuse, often transversely elongate, dark brown spot embedded in stripe just anterad of midpoint and another small, diffuse dark brown spot embedded in stripe immediately anterad of posterior margin; in females, T1 with some intermediately dense, intermediately long, golden setae, remainder of tergum devoid of long setae, in males, T1 and lateral surfaces of T2 with a dense covering of long, slender, golden setae, remainder of tergum devoid of long setae. *Sternum*. Base color dark brown, ventral surfaces of sternites often predominately yellow, pattern blotchy and irregular; surfaces mostly devoid of long setae, some intermediately long, wispy, pale gold setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3. *Pleural membrane*. In females, mostly devoid of long setae; in males, membrane of segment 2 with some long, wispy, brown setae, the remainder of membrane devoid of setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible. *Macerated specimens.* S9 apical margin very obtusely angled. Pulvini very reduced, poorly formed, hardly longer than broad, bearing numerous long, slender, brown setae. GPC somewhat weakly sclerotized; in lateral view dorsal margin basally slightly arched, subapically narrowly and shallowly notched, ventrally margin slightly irregular, dorsal and ventral margins convergent apicad; in ventral view broad laterally. Parameres sclerotized, in lateral view unproduced, in ventral view subtriangular, somewhat broad at base, breadth about half of length, lateral margin irregular, proximal margins weakly differentiated. Pelta sclerotized, very slender, proximally truncate, apically acuminate, like a narrow stylus.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distivalvae orange, ectoprocts orange and dark brown. *Macerated specimens.* Ventrovalvae elongate and somewhat narrow, subtriangular, length ca. two times width. Distivalvae in lateral view subtriangular. Linguella weakly produced, poorly sclerotized, bearing several short, slender, stiff, setae. Interdental space subtriangular, glabrous. Interdens sclerotized, somewhat small, nipple-like.

Variation. Vertex plates in the type specimen (JRJ_01628) are yellow.

Type material examined.—Holotype (A3 Fig. 16), male, Brazil, in BMNH collection: "Type /// Brazil /// iniquus /// iniquus WLK /// JRJ_01628". Condition: very good, antennae and wings spread, right antennae missing, a wooden splint inserted longitudinally through abdomen.

Additional material examined.—*Brazil*: Amazonas (INPA: 1 ♂, JRJ_00228, 1 ♀, JRJ_00232; SDMC: 1 ♂, JRJ_00230 [A3 Fig. 15]); Para (CMNH: 1 ♂, JRJ_00225; INPA: 1 ♂, JRJ_00231; SDEI: 1 ♂, JRJ_01702); Rondônia (FSCA: 3 ♂♂, JRJ_00226,

JRJ_00227, JRJ_00229; 2 ♀♀, JRJ_00238, JRJ_00239). *French Guiana*: St Laurent Du Maroni (BYUC: 1 ♂, JRJ_00180). *Country unknown*: (INPA: 1 ♀, JRJ_00242).

Morphology, biology and ecology.—Several male and female specimens were collected at MV and UV lights, at elevations of 40 to 230 m.

Discussion.—Gerstaercker's (1894) description of *Episperches irideus* does not conflict with characteristics of *iniqua*, and van der Weele (1909) considered the two conspecific. This is a rather bland species, essentially devoid of distinctive markings on the pleuron and notum in males and females, and lacking pruinescence in the males. Thus it is remarkable chiefly for lacking the diagnostic features of other species. Examination of more than a dozen specimens from various localities, however, reveals some shared unique features. In males, the pre-Mp_1 area margin is narrow and posteriorly more expanded than in other species, the medial triangle distal domain is slightly elongate, and the marginal cell row of the anal area has a few to several cells in distal half divided by crossveins, a feature unique in *Amoea*. Females from same locality are somewhat variable in coloring of thoracic pleuron, but match individuals from other sites in all other features.

Penny (1982) interpreted dissimilar pteronotal maculation patterns to be a single, plastic, species-level character ranging from unorganized spots to well-formed parasagittal stripes, and under this concept designated several diverse species as synonyms of *iniqua*.

While there does seem to some variation in the expression of pteronotal patterns within species named in this study, in each of the species there are several supporting characters that demonstrate the independence and holophyly of the species relative to other congeners. For example, in specimens of *arenosa*, the parasagittal stripes may be thin and very yellow with sharp edges to slightly broader and pale brown with more diffuse margins, and it is conceivable that in some specimens the stripes might be rather poorly expressed; however, the subalar stripe and the subtending stripe are consistently expressed, and the subalar setae are always thick. Shetlar (1977) also felt inclined to lump species, but such an inclination seems to have arisen from not having the type specimens available for examination, and having otherwise only a small quantity of material.

Amoea latipennis *(Navás, 1912)*

(A3 Figs. 17–18, 81)

Episperches latipennis Navás 1912

—Navás 1912b.10.31 r#542: 135 {OD: ♀, D, DIS. TS: not indicated [holotype]. TL: Guatemala. TR: MNHN. Type specimen examined (see "Type material examined" below).}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 12 {GD, L}

Etymology and nomenclatural notes.—*latipennis*: latus (Latin), 'broad, wide' + penna (Latin), 'feather, wing', = 'broad wing'. Perhaps named for what Navás (1912) observed to be the proportionally longer hind wing as compared to that of the similar species *vacua*; alternatively it could be for the breadth of the wing base in males (a feature of several *Amoea* species).

Diagnosis.—Pteronotal parasagittal stripes absent. Subalar stripe absent or narrow and only weakly developed, even less so in males, pale; remainder of thoracic pleuron strongly variegated, colors subdued. Subcostal veinlet 2 to approximately 7 or 8 margined with brown pigment, sometimes only thinly and diffusely; often most other veins, veinlets and crossveins thinly and diffusely margined, giving the wing a slightly darker appearance. Deltus completely filled with brown pigment. Males: pruinescent; abdominal tergum setae moderately dense, medium length, wispy white or pale yellow, progressively shortening toward apical segments; pleural membrane bearing a dense coat of short golden setae.

Autapomorphies.—entire wing venation margined; S3 with yellow macula present on anterior margin, remainder of sclerite evenly brown or dark; GPC without a dorsal notch.

Distribution.—Western Mexico south to Costa Rica.

Description.—

Size (mm). Male: length of body 26–32, abdomen 17–22, forewing 26–31, hind wing 24–26, antennae 17–19. Female: length of body 24–30, abdomen 16–22, forewing 28–36, hind wing 26–31, antennae 18–22.

Head. Breadth more or less coequal to that of mesothorax. Occiput pattern obscure, base color dark brown with texture of very fine, pale golden microsetae, lateral areas with irregular dark reddish brown and orangish-yellow maculations, similar in appearance to lateral plates of vertex. Vertex sandy yellowish or reddish brown; vertex plates nearly concolorous with vertex, reddish or dark brown to orangish-yellow; setae rather dense near antennae, golden-yellow anteriorly, posterodorsally and laterally with dark brown setae mixed in, transitioning to pale yellow posteriorly. Extra-torular sclerites dusky orange to dull brown, concolorous with upper portion of frons. Paraocular band dark brown, transitioning to yellow laterally and ventrally. Frons medium dusky yellowish or orange in ventral two-thirds, transitioning to dusky medium to dark brown in dorsal third; setae moderately dense, golden-yellow, lateral setae with tips becoming brownish. Clypeus orangish-yellow, some small or narrow diffuse reddish to brown maculations sometimes present laterally. Labrum concolorous with mesal portion of clypeus. Mandibles dull dark yellow basally, transitioning to very dark reddish-brown apically. Labium more or less concolorous with or perhaps slightly paler than labrum with a thin dark brown sagittal line. Eyes in anterior view symmetrically round, in lateral view larger in ventral half. Antennae flagellomere internodes pale to dark reddish brown, nodes dark reddish brown to dark brown; clubs medium to dark brown, mesal portion of anterior face often diffusely yellow or orange.

Thorax. In males, pruinescence often nearly completely covering thorax. *Cervix.* Dorsal cervical plates bearing long, slender, white setae. Cervical sclerite sandy or dull reddish-brown, sometimes darkening apically. *Pronotum.* Posterior flange posteror margin covering mesoacrotergite. Coloration of anterior flange and medial transverse band more or less evenly medium brown, posterior flange often predominately orange, posterior margin, at least mesally, dark brown, and this usually contiguous with a diffuse dark brown sagittal line. All surfaces with somewhat long, slender, very pale yellow to white setae.

Pteronotum. Usually dull pale to somewhat dark earthy brown with diffuse yellow or orange maculations, pattern often indistinct, but sometimes more conspicuous, often due to oily residues (from collection medium?), pruinescence in males often obscuring pattern, pattern as follows: maculations on lateral and posterior surfaces of anterolateral swellings of mesoprescutum, anterior face of lateral hemispheres of mesoscutum, anterior surfaces of mesoscutellum as sublateral teardrop-shaped maculae, anterolateral and mesal faces of transverse posterior swelling of meso- and metascutellum; velvety spots of metascutum dark brown, slightly darker than other surfaces of sclerite; entire surface of pteronotum covered with intermediately dense, medium length, fine, very pale brown, pale yellow, or white setae, in males setae appearing somewhat denser and wispy white on posterolateral surfaces and axillary cords. *Pleuron* with color pattern variably variegated dull brown and yellow, differing slightly in males and females; in males, pattern often completely obscured by pruinescence, appearing pale whitish yellow, but when not obscured usually more yellow than brown, with almost no hint of a subalar stripe; in females, pattern as in males, but sometimes yellow color becoming aggregated on sclerites subtending wing bases and appearing as a broad but irregular subalar stripe with an irregular ventral margin, sclerites below more predominately brown; all surfaces evenly covered with a somewhat dense coat of intermediately long, very slender, pale yellow to white setae, except slightly denser and directed posterad on mes- and metanepisternites, this accentuating the appearance of a weak subalar stripe in females.

Legs. Femora and tibiae predominately pale to dark dusky brown, femora slightly paler proximally, tibiae with proximal one-half to two-thirds of dorsal surface with a longitudinal yellow stripe, fascia yellow, surpassed or not by stripe. Tarsi dark reddish brown to almost black, apex of terminal tarsomere diffusely reddish, tibial spurs only very weakly curved, almost straight, posterior spur longer than anterior one and extending approximately to apex of second tarsomere, tibial spurs and tarsal claws pale to dark reddish-brown. Coxae with intermediately dense, medium length, slender, pale yellow to white setae; antennal comb setae predominately golden, black distally.

Wings. Dimension and shape. Intermediately broad, apically rounded, apices slightly more acute in males. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, cell width and height more or less coequal. Pterostigma with four to six forked and unforked brown veinlets; membrane cream to pale brown, sometimes weakly opaque; veins often thickened and appearing slightly margined. Deltus evenly dark brown, translucent to opaque. Presectoral area with eight, rarely nine, cells. Rs with four to five, usually five, forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. seven to nine irregular but more or less complete rows of cells. Cubital triangle distal domain with two cells . Anal area cell row with cells undivided by crossveins. *Color and patterning.* Venation medium to dark brown, usually dark brown; subcostal veinlet 2 to approximately 7 or 8 margined with brown pigment, sometimes only thinly and diffusely; often most other veins, veinlets and crossveins thinly and diffusely margined, helping to give the wing a slightly darker appearance. Membranes of entire wing often with very slight dusky hue. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with two to three (usually two) cells. Pre-Cup axillary disk dark brown, posterodistal margin narrowly devoid of pigment to slightly yellowish. Pre-Mp_1 area margin slightly expanded in females, greatly expanded in males. Anal area with two rows of undivided cells.

Abdomen. In males, reaching to pterostigma or slightly past when wings folded back; in females, usually not reaching to pterostigma, much shorter. *Tergum*. Base color dull dark brown, in males usually more or less evenly brown with pattern obscure, often a pair of very diffuse dark brown sublateral maculae positioned just anterad of midpoint and another pair just anterad of posterior margin; in females, often a pair of narrow, diffuse, cinnamon-colored parasagittal stripes expressed along full length, each tergite with a small, diffuse, round, dark brown spot embedded in stripe just anterad of midpoint and another immediately anterad of posterior margin; In females, T1 with moderately dense, intermediately long, wispy, pale yellow setae, A2 and T2 laterally with somewhat dense, moderately short, slender, pale yellow setae, remainder of tergum devoid of long setae, in males, T1 with a dense covering of long, wispy, pale yellow or white setae, T2 to ca. T4 with moderately dense, medium short, slender, pale yellow or white setae, these becoming very sparse and reduced on remainder of tergum. *Sternum*. Often more or less evenly brown, S2 usually more or less evenly dark brown but anterolateral surface with a small, diffuse, ovoid yellow macula, S3 anterior one-sixth often with a transverse, broadly almond-shaped macula, S3 to terminal sternite occasionally diffusely and patchily yellow; in females, surfaces mostly devoid of long setae, some intermediately long, wispy, pale yellow setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3; in males, as in females but somewhat denser, continuing nearly to apex of S3. *Pleural membrane*. In females, mostly devoid of long setae, some wispy pale yellow setae on membrane of segment 2; in males, a dense coat of medium short, very slender, pale yellow setae from base of abdomen to segments 5 or 6, becoming shorter and sparser on distal segments.

Male terminalia. Unmacerated specimens. GPC often slightly everted, apices of pulvini slightly protruding and visible. *Macerated specimens.* S9 apical margin obtusely angled. Pulvini relatively somewhat enlarged, weakly sclerotized, two to three times as long as width at base, nearly as long as GPC, bearing numerous long, somewhat slender, brown setae. GPC very weakly sclerotized; in lateral view dorsally entire, dorsal notch absent, ventrally slightly irregular, dorsal and ventral margins convergent apicad; in ventral view somewhat narrow laterally, longer than wide. Parameres sclerotized, in lateral view unproduced, in ventral view simple, appearing like cloven hooves, but not curved, proximal margins weakly differentiated. Pelta somewhat sclerotized, very narrowly almond-shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae, distivalvae, and ectoprocts dark brown, distivalvae sometimes slightly paler. *Macerated specimens.* Ventrovalvae elongate and somewhat narrow, subtriangular, length ca. two and a half times width. Distivalvae in lateral view subtriangular. Linguella weakly produced, poorly sclerotized, bearing several short, slender, stiff, setae. Interdental space rounded triangular, glabrous. Interdens sclerotized, somewhat small, cone- or nipple-like.

Variation. Some males are quite small. Specimens from more southerly collection localities express less darkened margining of the wing venation.

Type material examined.—Holotype, male, Guatemala, in MNHN collection: "MUSEUM PARIS GUATEMALA ENV. de GUATEMALA R. GUÉRIN 1908 /// TYPE /// LECTOTYPE /// Episperches latipennis type. Nav. /// Episperches latipennis Navás, 1912 Lectotype J. Legrand dét. 1991 /// JRJ_01222". Condition: fair, antennae and wings spread, FW broken, HW with posterior margins torn, right antennae and FW missing, pieces attached together with glue.

Additional material examined.—*Costa Rica*: Guanacaste (EMEC: 2 ♂♂, JRJ_00169, JRJ_00171; EMUS: 3 ♂♂, JRJ_00170, JRJ_00172, JRJ_00173). *Honduras*: Francisco Morazan (FSCA: 1 ♀, JRJ_00118). *Guatemala*: Izabal (FSCA: 1 ♂, JRJ_00117); Peten (JRJC: 1 ♂, JRJ_10123); Suchitepequez (WSU: 2 ♂♂, JRJ_01282 [A3 Fig. 21], JRJ_01283). *Mexico*: Chiapas (TAMU: 2 ♂♂, JRJ_00059, JRJ_00069; UCDC: 3 ♀♀, JRJ_00114 [A3 Fig. 18], JRJ_00115, JRJ_00116); Chihuahua (SDMC: 2 ♂♂, JRJ_00056, JRJ_00061); Chilpancingo (CMNH: 1 ♂, JRJ_00107 [A3 Fig. 17]; SDMC: 1 ♂, JRJ_00054; TAMU: 1 ♀, JRJ_00096); Jalisco (EMEC: 3 ♂♂, JRJ_00051, JRJ_00071, JRJ_00109; SDMC: 1 ♂, JRJ_00077); Morelos (EMEC: 1 ♂, JRJ_00113); Nayarit (SDMC: 16 ♂♂, JRJ_00053, JRJ_00055, JRJ_00057, JRJ_00060, JRJ_00062, JRJ_00063, JRJ_00064, JRJ_00065, JRJ_00067, JRJ_00070, JRJ_00072, JRJ_00073, JRJ_00074, JRJ_00075, JRJ_00076, JRJ_00108; 21 ♀♀, JRJ_00079, JRJ_00080, JRJ_00081, JRJ_00082, JRJ_00083, JRJ_00084, JRJ_00085, JRJ_00086, JRJ_00087, JRJ_00088, JRJ_ 00089, JRJ_00090, JRJ_00092, JRJ_00098, JRJ_00100, JRJ_00101, JRJ_00102, JRJ_00103, JRJ_00104, JRJ_00105, JRJ_00106); Oaxaca (BYUC: 2 ♂♂, JRJ_00066, JRJ_00110; SDMC: 1 ♂, JRJ_00111, 1 ♀, JRJ_00097; TAMU: 1 ♂, JRJ_00068); Sinaloa (EMEC: 1 ♂, JRJ_00112; MSUC: 1 ♂, JRJ_00052, 4 ♀♀, JRJ_00091, JRJ_00093, JRJ_00095, JRJ_00099; USNM: 2 ♂♂, JRJ_00058, JRJ_00078). *Nicaragua*: Granada (EMEC: 2 ♂♂, JRJ_00119, JRJ_00120).

Morphology, biology and ecology.—Male and female loan specimens were collected at MV and UV lights. Habitat reported on labels include thorn scrub along a river at 700 m in Guerrero, Mexico, pine-oak forest at 850 m in Chiapas, Mexico, tropical deciduous/pine-oak transitional forest at 1200 m in Chiapas, and thorn scrub at 600 m in Guatemala. Collection elevations ranged from 130 to 1400 m.

Discussion.—This species is very similar to *vacua* and can be difficult to distinguish, particularly among specimens originating in southern Mexico and Central America. In central and northern Mexico, the species are more physically distinct, and *latipennis* occurs primarily in the west, whereas *vacua* occurs principally in the east.

Navás's type specimen in the MNHN was designated by J. LeGrand as lectotype, but the original description seems to imply only a single specimen was examined.

Amoea nivea *Navás, 1911*

(A3 Fig. 19, 82)

Amoea nivea Navás, 1911

—Navás 1911 r#535: 23, fig. 1 {OD: ♂, TS: not indicated [implied syntypes: ♂♂—a lectotype needs to be designated from syntype material]. TL: Paraguay. TR: ZSM. Type specimens not examined (see "Discussion" below).}

—Navás 1912b.10.31 r#542: 209, fig. 2.[a] {D, GD, K}

—Navás 1913 r#1207: 49, fig. 5 {D, GD, K}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 11 {GD, L}

Etymology and nomenclatural notes.—*nivea*: nivea (Latin), 'snowy, as white as snow'. Named for the setae arising from T1 in males, which Navás (1911) described as "niveis" ('snow-white').

Diagnosis.—Notal parasagittal stripes absent. Subalar stripe absent, or very weakly hinted at and broad; thoracic pleuron diffusely variegated, predominantly pale yellow or orangish. Males: Not pruinescent. Some individuals (Bolivia) with wings distinctly melanistic. HW base much less expanded than in other species. S1 with erect white setae. Tergum setae moderately sparse, medium length but quickly shortening, golden, reducing to nearly glabrous after T3. Pleural membrane setae intermediately dense, short, very slightly robust, dark brown, reducing distally. Female: Unknown.

Autapomorphies.—male HW basiposterior margin expanded and convex after angle, but much less so than in other species, weakly changing angle at Mp_1; male T1 setae dense, medium long, stiff, white, dorsomesally erect.

Distribution.—Bolivia; Ecuador; Paraguay; Peru.

Description.—

Size (mm). Male: length of body 29–30, abdomen 19–20, forewing 27–30, hind wing 24–25, antennae 18–19. Female: length of body 28, abdomen 19, forewing 34, hind wing 30, antennae 20.

Head. Breadth more or less coequal to that of mesothorax. Occiput with an irregular and often obscured pattern of dark brown and dull diffuse yellow maculations. Vertex sandy to dark dusky brown; plates dark brown to grayish-yellow; setae rather dense near antennae, golden yellow with some dark brown setae mixed in anteriorly and dorsally, transitioning to just golden yellow to dark brown posteriorly. Extra-torular sclerites dusky orange to brown, often concolorous with prefrons and dorsal most portions of paraocular band laterad of antennal bases. Paraocular band dark brown laterad of antennae, transitioning to yellow adjacent to frons. Orbital sclerite yellow or brown. Frons medium to dark dusky orange; setae moderately dense, dark golden-brown. Clypeus pale to dusky yellow, laterally often with very diffuse reddish-brown maculations. Labrum pale dull orangish-yellow. Mandibles concolorous with clypeus basally, transitioning to very dark reddish-brown apically. Labium pale to orangish-yellow, with a thin dark brown sagittal line. Eyes in anterior view symmetrically round, in lateral view very slightly larger in ventral half. Antennae flagellomere internodes yellowish or reddish to dark brown, nodes narrowly pale; clubs dark brown, often with a diffuse orange stripe on anterior face.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, golden brown setae. Cervical sclerite evenly dark brown. *Pronotum.* Posterior flange posteror margin not quite or just barely covering mesoacrotergite. Pronotum coloration more or less evenly dark brown, posterior flange sometimes evenly dark brown, usually sublaterally diffusely dark reddish- or orangish-brown, these areas separated by a broad diffuse sagittal dark brown stripe and entire posterior margin broadly dark brown. All surfaces with medium to somewhat long, slender, brown to golden brown setae. *Pteronotum*. More or less evenly brown to dark brown, anterolateral faces of mesoprescutum narrowly diffusely yellow or orange, anterior surface of posterior transverse swelling of mesoscutellum sometimes with very diffuse lateral and mesal dull orangish maculae; velvety spots of metascutum dark brown, darker than other surfaces of sclerite; entire surface of pteronotum covered with moderately dense, intermediately long, very fine, golden brown setae, setae somewhat denser and longer on posterolateral surfaces of mesoscutum, mesoscutellum, metascutum, and metascutellum. *Pleuron* with color variegated; in males, almost completely yellow; female specimen stained, unclear; all surfaces more or less evenly covered with a somewhat dense coat of moderately short, very slender, pale yellow setae.

Legs. Femora and tibiae with color variable, femora proximally pale yellow, transitioning to dusky brown distally, tibiae with anterolateral faces and sometimes entire surface dusky dark brown. Tarsi dark reddish-brown to black, apex of terminal tarsomere diffusely yellowish or reddish, tibial spurs only very weakly curved, almost straight, not extending past apex of second tarsomere, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, very pale yellow setae; antennal comb setae predominately golden, black distally.

Wings. Dimension and shape. Intermediately broad, apically rounded, very slightly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal. Pterostigma with four to five forked and unforked brown veinlets; membrane cream yellow to brownish, often opaque; veins often thickened and thinly margined. Deltus completely filled with yellowish to pale brown pigment, this usually darkened mesally, sometimes anteromesally, color sometimes fainter proximally, in melanistic males pigment very dark. Presectoral area with eight cells. Rs with six forks. Mp_2 + Cua_1 evenly curving toward hind margin in distal portion. Cubital area with ca. seven to nine irregular but more or less complete rows of cells. Cubital triangle distal domain with two cells . Anal area cell row with cells undivided by crossveins. *Color and patterning.* Venation medium to dark brown. Membranes of wing usually completely lacking pigment, some males distinctly melanistic with membranes strongly tinged with brown color. HW. As in forewing except as follows. Mp_2 fork angle nearly 90°. Medial triangle distal domain with two cells. Pre-Cup axillary disk dark brown. a small distal portion translucent to pale yellow. Pre-Mp_1 area margin only very slightly expanded in males and females, HW base of males thus much narrower than in all other species. Anal area with two rows of cells.

Abdomen. In males reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Often evenly dark brown, sometimes with a pair of broad diffuse dark orange to reddish parasagittal stripes; female T1 with some intermediately dense, intermediately long, golden setae, remainder of tergum devoid of long setae, in males, T1 bearing a dense covering of erect, long, slender white setae, these directed slightly mesad, T2 to T4 with a somewhat dense covering of medium short, slender, gold setae, these becoming shorter and more sparse distally, remainder of tergum devoid of long setae. *Sternum*. Base color dark brown, ventral surfaces of sternites varying from evenly brown to predominately yellow with pattern blotchy and irregular; surfaces mostly devoid of long setae, some intermediately long, wispy, pale gold setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3. *Pleural membrane*. In females, mostly devoid of long setae; in males, membrane from segment 2 to 4 with a dense covering of short, very slender, brown setae, the remainder of membrane devoid of setae.

Male terminalia. Unmacerated specimens. GPC everted or not, pulvini often barely visible. *Macerated specimens.* S9 apical margin obtusely angled. Pulvini moderately small but well developed, somewhat sclerotized, two to three times as long as width at base, bearing numerous intermediately long, somewhat slender, brown setae. GPC somewhat sclerotized; in lateral view dorsal margin more or less entire, mesally narrowly and very shallowly notched, ventral margin slightly irregular, dorsal and ventral margins slightly convergent apicad; in ventral view only intermediately broad laterally. Parameres sclerotized, in lateral view unproduced, in ventral view narrowly triangular, breadth at base about one-third of length, apicolateral margin irregular, proximal margins weakly differentiated. Pelta sclerotized, slender, proximally slightly rounded, apically acuminate.

Female terminalia. Unmacerated specimens. Specimen discolored, all surfaces appearing very dark brown. *Macerated specimens.* Unavailable.

Variation. Melanistic males with costal areas strongly fuscous.

Type material examined.—Type specimen(s) not available for examination.

Additional material examined.—*Bolivia*: Beni (CMNH: 1 ♂, JRJ_00220 [A3 Fig. 19]); Santa Cruz (FSCA: 3 ♂♂, JRJ_00221, JRJ_00222, JRJ_00223). *Brazil*: Rondônia (FSCA: 1 ♀, JRJ_00237). *Ecuador*: Orellana (EMUS: 1 ♂, JRJ_00216). *Paraguay*: Paraguari (USNM: 1 ♂, JRJ_00224). *Peru*: Madre de Dios (FSCA: 1 ♂, JRJ_00217; USNM: 2 ♂♂, JRJ_00218, JRJ_00219).

Morphology, biology and ecology.—Specimens were collected in “subtropical moist forest” at 290 m in Peru and ‘tropical transition forest’ at 430 m in Bolivia. Another specimen was collected at 250 m in Peru.

Discussion.—A handful of specimens available for this study unambiguously matched Navás’s (1911) photograph and description. The photograph as it appears in scanned reproductions of the original paper is rather dark and appears more as a silhouette; nevertheless, the narrow hind wing and dark tint of the wing membranes, both diagnostic for this species, are clearly evident. Navás also indicates that the dorsal setae on T1 and T2 are snowy white (“Abdomen…basi fusco-fulvo pilosum, inferne segmentis 1–2 totis niveis”), another diagnostic feature.

Not all of the specimens examined were melanistic; those with dark wings all came from the same locality, Santa Cruz, Bolivia (-17.866667°, -63.000000°), a more south-central location within the known range. Navás’ melanistic specimen originated from Paraguay, also in the southern part of the range.

A specimen (JRJ_00237) was determined to probably represent the female of *nivea* based on wing shape, distribution, and an absence of diagnostic features that would ally it to other possibly species from the same geographic region, but its thorax coloration is obscured by oils and crucial diagnostic features are difficult to discern. The specimen has a strange longitudinal 3/4 yellow stripe on the anterior portion of the pleuron, but the shape and color could be an artifact of the residue. Males of *nivea* lack stripes.

Amoea periculosa *new species*

(A3 Fig. 20, 80)

Etymology and nomenclatural notes.—*periculosa*: periculosus (Latin), 'dangerous, perilous'. Named for the striking intensity and contrast of the pleural coloration in females of many specimens, reminiscent of a hazard pattern.

Diagnosis.—Pteronotal parasagittal stripes absent. Subalar stripe present, well-developed, distinctly yellow; thoracic pleuron otherwise dark brown, sometimes paler or yellowish around coxae. Wing veins dark brown, but not margined. Wing basal sclerites and membranes dark brown, often opaque. Deltus filled with pigment, this brown to very dark brown and often opaque anterobasally, becoming lighter brown and translucent posterodistally.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Bolivia; Brazil; Ecuador; French Guiana; Peru.

Description.—

Size (mm). Male: length of body 27, abdomen 18, forewing 30, hind wing 26, antennae 19. Female: length of body 24–28, abdomen 15–21, forewing 32–37, hind wing 29–33, antennae 20–22.

Head. Breadth more or less coequal to that of mesothorax. Occiput dark brown, lateral margin with a subtriangular yellow macula. Vertex dark brown; plates dark brown; setae rather dense near antennae, mixed golden yellow and dark brown anteriorly and dorsally, transitioning to pale golden brown posteriorly. Extra-torular sclerites dusky to dark brown. Paraocular band dark dusky brown adjacent to antennae, transitioning to dull dark yellowish brown ventrally. Frons dark dusky orange; setae dense, golden yellow at base, apices dark brown. Clypeus pale to dark yellow or orange, with large, irregular, diffuse reddish-brown maculations laterally, a very diffuse, sagittal reddish-brown line often present, sometimes continuing onto labrum. Labrum concolorous with mesal portion of clypeus. Mandibles bases concolorous with labrum, transitioning to very dark reddish-brown apically. Labium pale yellow, slightly paler than mandible base and labrum, with a thin dark brown sagittal line. Eyes slightly larger in ventral half. Antennae flagellomere internodes dull pale to dark reddish-brown, nodes dark brown; clubs medium to dark brown, often with a diffuse broad yellow stripe on anterior face.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, pale yellow setae. Cervical sclerite evenly dull dark brown. *Pronotum.* Posterior flange posteror margin barely covering mesoacrotergite. Pronotum coloration more or less evenly dark brown, posterior flange base color dark brown, sublaterally yellowish-orange, mesoposterior margin broadly dark brown, a variably broad dark brown sagittal stripe present. All surfaces with medium to somewhat long, slender, golden brown setae. *Pteronotum*. Dark earthy brown, pattern somewhat subdued, a diffuse orange macula on lateral surface of anterolateral swelling of mesoprescutum, mesoanterior face of lateral hemisphere of mesoscutum, anterolateral and mesal faces of transverse posterior swelling of mesoscutellum; velvety spots of metascutum dark cinnamon brown; in females, entire surface covered with intermediately dense, somewhat short, fine, golden brown setae, in male, as in females, but lateral and posterior surfaces with setae becoming denser and whiter, posterior margin of meso- and metascutellum with a loose fringe of medium length, slender, pale golden yellow or white setae. *Pleuron* in females, a broad, yolk yellow subalar stripe present, ventral margin of stripe well defined, remainder of pleuron dark brown, with membranes and a few small areas with diffuse yellow maculations; surfaces with more or less even coat of moderately dense, very fine, pale golden brown setae, these becoming denser, slightly longer, and white along subalar stripe; in male, subalar stripe absent, surfaces variegated dull yolk yellow and dark brown, predominately yellow in area of subalar stripe, setae as in females, but somewhat denser and whiter.

Legs. Femora and tibiae color patterning rather variable, sometimes completely dark dusky brown, at other times with some surfaces yellow, as follows: femora yellow in proximal half, diffusely transitioning to dusky dark brown, this continuing onto tibiae, fascia yellow, posterolateral surface of tibiae yellow, sometimes only in distal two-thirds. Tarsi dark brown, almost black, tibial spurs only very weakly curved, almost straight, posterior spur longer than anterior one and not extending past apex of third tarsomere on pro- and mesothoracic tibiae, second tarsomere on metathoracic tibia, tibial spurs and tarsal claws dark reddish-brown. Coxae with intermediately dense, medium length, slender, pale yellow setae; antennal comb setae predominately golden, in male black along posterolateral margin of setal patch.

Wings. Dimension and shape. Intermediately broad, apically very subtly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal. Pterostigma with four to five forked and unforked dark brown veinlets; membrane translucent, with a tinge of brown color; veins often slightly thickened and appearing very thinly margined. Deltus yellowish to dark brown, often darker anteromesally, sometimes completely opaque. Presectoral area with eight cells. Rs with six forks. Mp_2 + Cua_1 evenly curving toward hind margin in distal portion. Cubital area with ca. eight to nine irregular but more or less complete rows of cells. Cubital triangle distal domain with two cells . Anal area cell row with cells undivided by crossveins. *Color and patterning.* Venation dark brown. Membranes of wing in females completely lacking pigment, in male membranes with a very slight brownish tinge. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with two to three cells, elongate and narrowed in male. Pre-Cup axillary disk completely dark brown. Pre-Mp_1 area margin slightly expanded in females, greatly expanded in male. Anal area with two rows of undivided cells.

Abdomen. In male reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Base color dull dark brown, in females, vestiges of broad cinnamon to sometimes orangish colored parasagittal stripes present, sometimes a pair of very diffuse, dark brown parasagittal spots positioned immediately anterad of posterior margin of T3 to T7, T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, golden brown setae, remainder of tergum devoid of long setae; in male, pattern as in females, but very obscured, T1 with a dense covering of long, slender, white setae, T2 to T5 with a somewhat dense covering of very short, slender, whitish to pale yellow setae. *Sternum*. Base color dark brown, S1 and S2 sometimes with yellow maculations, S3 anterior one-sixth often with a transverse, broadly almond-shaped yellow macula, S3 to terminal sternite occasionally diffusely and patchily yellow; surfaces mostly devoid of long setae, some intermediately long, wispy, pale gold setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3, setae longer and denser in male.

Pleural membrane. In females, mostly devoid of long setae; in male, membranes of segment 2 to ca. segment 5 with a dense coat of short, slender, golden brown setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible, ectroprocts and S9 completely dark brown. *Macerated specimens.* Unavailable.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distivalvae dusky dark yellowish-brown, ectoprocts dark brown, distal margins diffusely yellowish. *Macerated specimens.* Ventrovalvae elongate and somewhat narrow, subtriangular, length ca. two and a half to three times width. Distivalvae in lateral view subtriangular.

Linguella not produced or sclerotized, bearing several short, slender, stiff, setae. Interdental space subtriangular, glabrous. Interdens sclerotized, cone- or nipple-like, apex with a few very short slender setae.

Variation. Specimens from the northeast reaches of the geographic distribution overall with slightly darker pteronota and less intense notal maculations.

Type material examined.—*Holotype*, **new designation**, female, Peru, in USNM collection: "PERU: Madre de Dios: Manu; Pakitza (12° 7' S 70° 58' W) 250m 9-23 Sep 1988 O. Flint & N. Adams /// HOLOTYPE Amoea periculosa Jones ♀ design. J. R. Jones 2014 /// JRJ_00186". Condition: excellent; antennae and wings spread, no parts missing.

Additional material examined.—*Bolivia*: La Paz Dept (USNM: 1 ♀, JRJ_00187); Santa Cruz (FSCA: 1 ♀, JRJ_00188; MFNB: 2 ♀♀, JRJ_00189, JRJ_01705). *Brazil*: Amazonas (INPA: 1 ♀, JRJ_00184); Roraima (INPA: 1 ♀, JRJ_00185). *Ecuador*: Orellana (EMUS: 1 ♀, JRJ_00183). *French Guiana*: Cayenne (FSCA: 1 ♂, JRJ_00191 [A3 Fig. 20], 3 ♀♀, JRJ_00182, JRJ_00192, JRJ_00193). *Guyana*: Potaro Siparuni (SEMC: 1 ♀, JRJ_00181).

Morphology, biology and ecology.—Labels on loan material indicate several specimens were taken at UV and MV lights. One specimen was collected in "tropical transition forest" in Bolivia. Recorded elevations range from ca. 50 to 250 m.

Discussion.—This species is very similar to *flavitaenia* but differs in having much more intense thorax coloration in the females, and in males having the subalar stripe only weakly expressed, pleural setae pale and moderately thick, in lacking pruinescence, and in the pre-Mp_1 area margin being more expanded. In several females from French Guiana, the thorax base color is very dark brown, almost black, and the subalar stripe is intensely yellow. In these same specimens the basal wing sclerites and venation are very dark brown to almost black, and the deltus is very dark brown and opaque. Not all specimens have the brown coloration quite as dark. In general, females of *periculosa* are also smaller (FW 32–37 mm) than those of *flavitaenia* (FW 36–40 mm).

Amoea vacua *(Gerstaecker, 1894)*

(A3 Figs. 21–22, 81)

Haploglenius vacuus Gerstaecker, 1894

—Gerstaecker 1894 r#2559: 95 {OD: indicated as ♂♀ [but see van der Weele 1906], D. TS: not indicated [syntypes: 2 ♀♀—see van der Weele 1906; a lectotype needs to be designated from syntype material]. TL: Honduras. TR: not indicated [EMAU—see van der Weele 1909, fig. 11 caption]. Type specimen not examined (see "Discussion" below).}

—van der Weele 1906 r#404: 227 {TS}

—van der Weele 1909.01.05 r#420: 39 {SYN}

—Navás 1912a.06.?? r#549: 3 {MOR}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 12 {SYN}

—Oswald and Penny 1991.12.02 r#7138: 8 {TSP (of *Episperches* Gerstaecker—citation of incorrect designation by Penny 1982a)}

Episperches vacuus (Gerstaecker, 1894)

—van der Weele 1909.01.05 r#420: 39, figs. 11, 12, 13 {DIS, GD, RD: ♂♀, SYN, TS}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 12 {GD, L, SYN}

—Penny 1982a r#5105: 395 {TSP (of *Episperches* Gerstaecker; incorrect designation—see Oswald and Penny 1991)}

Amoea vacuus (Gerstaecker, 1894)

—Penny 2002.10.21 r#10230: 177, fig. 6 {AD, D, FP, GD, H, NC}

Etymology and nomenclatural notes.—*vacua*: vacuus (Latin), ‘empty space, void’. Gerstaecker provided no explanation for the selection of this name in the original description.

Diagnosis.—Pteronotal parasagittal stripes absent. Subalar stripe absent; thoracic pleuron strongly variegated, colors subdued. Wing veins not margined. Deltus mostly completely filled with brown pigment, but pigment absent or distinctly yellowed and thin at junction of R and 1r-m. Males: pruinescent; abdominal tergum setae moderately dense, medium length, wispy white or pale yellow, progressively shortening toward apical segments; pleural membrane bearing a dense coat of short golden setae.

Autapomorphies.—basal cell of HW costal area almost completely devoid of dark color and sclerotization.

Distribution.—Eastern Mexico south to Costa Rica, U.S.: Utah.

Description.—

Size (mm). Male: length of body 28–33, abdomen 18–23, forewing 29–32, hind wing 24–28, antennae 19–22. Female: length of body 27–32, abdomen 19–21, forewing 33–36, hind wing 28–31, antennae 20–22.

Head. Breadth more or less coequal to that of mesothorax. Occiput pattern often obscure, base color dark reddish-brown, mesolateral margin with a more or less triangular yellow macula, sometimes other small yellow maculations present. Vertex sandy brown or reddish yellow with a texture of very fine, golden microsetae; plates nearly concolorous with vertex, reddish- or yellowish-brown; setae rather dense near antennae, golden anteriorly, dorso laterally with very dark brown setae mixed in, transitioning to pale yellow or white posteriorly. Extra-torular sclerites dusky orange to dull brown, concolorous with prefrons and upper portion of paraocular band. Paraocular band yellowish to dark brown laterad of antennae, transitioning to yellow laterally and ventrally. Frons dusky orange; setae moderately dense, golden, dorsolateral setae with tips becoming brownish. Clypeus yellow, some small or narrow diffuse reddish to brown maculations sometimes present laterally, rarely with a narrow diffuse red or dark brown sagittal line. Labrum concolorous with mesal portion of clypeus. Mandibles dull yellow basally, transitioning to very dark reddish-brown apically. Labium more or less concolorous with or perhaps slightly paler than labrum with a thin dark brown sagittal line. Eyes slightly larger in ventral half. Antennae flagellomere internodes pale to dark reddish brown, nodes dark reddish brown to dark brown; clubs medium to dark brown on all surfaces.

Thorax. In males, pruinescence often nearly completely covering thorax. *Cervix.* Dorsal cervical plates bearing long, slender, pale yellow or white setae. Cervical sclerite sandy or dull reddish to dark brown, slightly darker on anterodorsal faces and apically. *Pronotum.* Posterior flange posteror margin just covering mesoacrotergite. Coloration of anterior flange and medial transverse band more or less evenly medium yellowish- or reddish-brown, posterior flange sometimes more or less evenly dark brown, with pattern obscure, but often predominately yellow or orange, posterior margin, at least mesally, dark brown, and this usually contiguous with a diffuse dark brown sagittal line. All surfaces with somewhat long, slender, very pale yellow to white setae dorsally, transitioning to golden or brownish laterally. *Pteronotum*. Dull pale to slightly yellowish or evenly medium brown with very diffuse yellow or orange maculations, pattern sometimes indistinct, but often more conspicuous; pattern as follows: maculations on lateral and posterior surfaces of anterolateral swellings of mesoprescutum, mesoanterior face of lateral hemispheres of mesoscutum, anterolateral and mesal faces of transverse posterior swelling of meso- and metascutellum; velvety spots of metascutum cinnamon-colored to dark brown; entire surface of pteronotum covered with somewhat dense, medium length, fine, golden brown (in females) or white (in males) setae, in males setae denser and wispy white on posterolateral surfaces, pale yellow on axillary cords. *Pleuron* somewhat variably variegated dull brown and yellow, more yellow than brown, with no hint of a subalar stripe; all surfaces more or less evenly covered with a somewhat dense coat of moderately long, very slender, pale yellow to white setae.

Legs. Femora and tibiae with color somewhat variable, diffusely pale yellowish to dusky brown, femora sometimes very slightly paler proximally, tibiae sometimes with fascia yellow. Tarsi yellowish to reddish brown, tibial spurs only very weakly curved, almost straight, posterior spur longer than anterior one and extending approximately to apex of second tarsomere, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, pale yellow to white setae; antennal comb setae coppery-gold.

Wings. Dimension and shape. Intermediately broad, apically rounded, apices slightly more acute in males. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, cell width and height more or less coequal in proximal half, becoming slightly narrower than high in distal half. Pterostigma with four to six forked and unforked brown veinlets; membrane colorless or cream to pale brown, sometimes opaque; veins often thickened and margined with dark brown pigment. Deltus mostly brown but pigment absent or yellowish anteroproximally, usually more or less translucent, occasionally becoming opaque. Presectoral area with eight cells. Rs with six forks. $Mp_2 + Cua_1$ somewhat evenly curving toward hind margin in distal portion. Cubital area with ca. eight to ten irregular but more or less complete rows of cells. Cubital triangle distal domain with two cells . Anal area cell row with cells undivided by crossveins. *Color and patterning.* Venation pale to dark brown; subcostal veinlets unmargined; other veins, veinlets and crossveins also unmargined. Membranes of entire wing in males often with slight dusky tint and costal area somewhat darkened. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with two to three (usually two) cells, these slightly elongate and narrow in males. Pre-Cup axillary disk narrow, dark brown, posterodistal margin narrowly devoid of pigment to slightly yellowish. Pre-Mp_1 area margin slightly expanded in females, greatly expanded in males. Anal area with two rows of undivided cells.

Abdomen. In males, reaching to pterostigma or slightly past when wings folded back; in females, usually not reaching to pterostigma, much shorter. *Tergum*. Base color dull dark brown, a pair of narrow, cinnamon-colored parasagittal stripes expressed along full length, each tergite with a small, round, dark brown spot embedded in stripe just anterad of midpoint and another immediately anterad of posterior margin; In females, T1 with moderately dense, intermediately long, wispy, pale yellow setae, A2 and T2 laterally with somewhat dense, moderately short, slender, pale yellow setae, remainder of tergum devoid of long setae, in males, T1 with a dense covering of long, wispy, pale yellow or white setae, T2 to ca. T3 with moderately dense, medium short, slender, pale yellow or white setae, these more sparse dorsally and becoming more sparse and reduced on remainder of tergum. *Sternum*. Often more or less evenly dark brown, S1 and S2 anterolateral membranes usually yellow, S2 anterolateral surface often with a small, diffuse, ovoid yellow macula, S3 anterior one-sixth often with a transverse, broadly almond-shaped macula, S3 to terminal sternite occasionally diffusely and patchily yellow; in females, surfaces mostly devoid of long setae, some intermediately long, wispy, golden yellow setae on proximal membrane of S1, entire surface of S2, and proximal portions of S3; in males, as in females but somewhat denser, continuing nearly to apex of S3. *Pleural membrane*. In females, mostly devoid of long setae, some wispy golden yellow setae on membrane of segment 2; in males, a dense coat of medium short, very slender, golden yellow setae from base of abdomen to segments 4 or 5, becoming shorter and sparser on distal segments.

Male terminalia. Unmacerated specimens. GPC often slightly everted, apical margin of ectoprocts and S9 orangish. *Macerated specimens.* S9 apical margin obtusely angled. Pulvini small, somewhat sclerotized, one and a half to two times as long as width at base, less than one-third as long as dorsal portion of GPC, bearing numerous long, very slender, brown setae. GPC weakly sclerotized; in lateral view dorsally subapically weakly notched, ventrally very slightly irregular, dorsal and ventral margins convergent apicad; in ventral view somewhat narrow laterally, longer than wide. Parameres moderately sclerotized, in lateral view narrow, unproduced, in ventral view simple, narrowly triangular, breadth at base about one-third of length, apicolateral margin irregular, proximal margins somewhat well differentiated. Pelta moderately sclerotized, narrowly lens- or spindle-shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distivalvae and ectoprocts distally yellow. *Macerated specimens.* Ventrovalvae elongate and somewhat narrow, subtriangular, length ca. two times width. Distivalvae in lateral view subtriangular. Linguella very weakly produced, membranous, not protuding, bearing a few short, slender, stiff, setae. Interdental space diamond-shaped, glabrous. Interdens sclerotized, somewhat short, small, nipple-like; apex with or without four to five short, fine setae.

Variation. Depth of notch on dorsal margin of GPC is somewhat variable.

Type material examined.—The syntypes were not available for this study.

Additional material examined.—*Belize*: Stann Creek (FSCA: 1 ♂, JRJ_00152). *Costa Rica*: Guanacaste (EMEC: 1 ♀, JRJ_00166); San Jose (EMEC: 2 ♂♂, JRJ_00167, JRJ_00168). *Guatemala*: Suchitepequez (WSU: 1 ♀, JRJ_01285); Zacapa (WSU: 1 ♀, JRJ_01284). *Honduras*: Cortés (CAS: 1 ♀, JRJ_00163; MNHN: 1 ♂, JRJ_01614; NMW: 8 ♂♂, JRJ_00153, JRJ_00154, JRJ_00155, JRJ_00156, JRJ_00157, JRJ_00158, JRJ_00164, JRJ_00165, 4 ♀♀, JRJ_00159 [A3 Fig. 22], JRJ_00160, JRJ_00161, JRJ_00162). *Mexico*: Chiapas (TAMU: 1 ♀, JRJ_00150); Federal (USNM: 1 ♂, JRJ_00125); San Luis Potosi (TAMU: 1 ♀, JRJ_00142); Tamaulipas (FSCA: 1 ♀, JRJ_00143; TAMU: 2 ♂♂, JRJ_00132, JRJ_00133); Veracruz (EMEC: 1 ♂,

JRJ_00136; FSCA: 3 ♂♂, JRJ_00122, JRJ_00123, JRJ_00137; TAMU: 1 ♂, JRJ_00124, 2 ♀♀, JRJ_00145, JRJ_00149; UCDC: 2 ♀♀, JRJ_00141, JRJ_00151); Yucatan (FSCA: 8 ♂♂, JRJ_00126, JRJ_00127, JRJ_00128, JRJ_00129, JRJ_00130, JRJ_00131, JRJ_00134, JRJ_00135, 6 ♀♀, JRJ_00138, JRJ_00140, JRJ_00144, JRJ_00146, JRJ_00147, JRJ_00148). *USA*: Utah (TAMU: 1 ♂, JRJ_00121). *Country unknown*: (FSCA: 1 ♀, JRJ_00139. MFNB: 4 ♀♀, JRJ_01697, JRJ_01638, JRJ_01699, JRJ_01700).

Morphology, biology and ecology.—Numerous loan specimens were collected at lights, including UV lights. Collection elevations given range from ca. 300-1050 m. One specimen was collected by sweeping vegetation in Suchitepequez, Guatemala, and another was captured "dead in spider web at light" in San Luis Potosi, Mexico.

Discussion.—Gerstaecker's (1894) original description alone cannot indubitably be connected to only one of the three very similar species of *Amoea* occurring in Honduras. The best clue he provides is his statement that the side of the thorax is yolk-yellow. But he does not clearly indicated if the yellow color is concentrated into a subalar stripe or not. Van der Weele (1909) was able to examine Gerstaecker's type material, along with a long series of additional males and females from San Pedro Sula, Honduras, which he labeled. At least some of that series (e.g., JRJ_00153–00165) were examined for this study, helping to confirm the taxonomic concept of *vacua*.

Van der Weele (1909) indicated that several specimens he examined bore labels recorded with the locality “Bahia”. Four of these from the MFNB collection (JRJ_01697–01700), were examined for this study, and they do appear to be females of *vacua*. Van der Weele did not explain how he knew those specimens are mislabeled, but they originate from the collection of Fruhstorfer, as does the long series of males and females from San Pedro Sula.

Concerning Gerstaecker’s type, Van der Weele (1909) states that the original description was based on two females, a larger and a smaller specimen, and that Gerstaecker mistakenly interpreted the smaller one to be a male, but in fact both specimens are females. Van der Weele states that the smaller individual has eggs attached to the slender abdomen. He further explains that the other female is very large and has the prothorax torn apart.

A single TAMU specimen bears a label with the collection locality given as Dixie National Forest, Utah. Aside from the location itself, there is no direct evidence yet to indicate that this outlying record has been mislabeled. The collection site, however, occurs ca. 2000 km from the next northernmost record, in northeastern Mexico.

Removed from Amoea

Ameropterus molinai (Navás, 1909) **new combination**

Episperches molinai Navás, 1909

—Navás 1909 r#1198: 55, fig. 1.[a] {OD: sex not indicated, ET. TS: not indicated [holotype]. TL: Colombia. TR: not indicated (private collection of Navás: remnants in MZBS—see Oswald 2013a). Type specimen not examined (see "Discussion" below).}

—Navás 1912b.10.31 r#542: 211 {D, GD, K}

—Navás 1913 r#1207: 51 {D, GD, K}

—Shetlar 1977 r#5727: 79 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus immaculatus* Olivier)}

—Penny 1978.09.15 r#5098: 12 {GD, L}

Etymology and nomenclatural notes.—*Molinai:* Latinized noun in the genitive case; named for Rdo. P. Juan de Molina, a Chilean naturalist (and possible collector of the type specimen).

Discussion.—No specimens in loan material available for this study matched Navás' figures or description, and essentially no specimens of *Amoea* (and only a handful of specimens of a few other entire-eyed haplogleniine species) were obtained which originated from Colombia (a single *Amoea* specimen labeled “New Granada” does not match Navás’ description).

Navás’ description of *molinai* was his first of a species of *Amoea* or *Episperches* and his only one with an essentially complete drawing of both wings. From his description and drawing, the following characters can be observed which conflict with all other known species of *Amoea*: the anterior and posterior margins of wings essentially parallel across most of length; pterostigmata opaque, dark; apical area with only two rows of cells; FW presectoral area with only 6 cells; poorly developed distal domain in HW medial triangle; second cell row posterad of Cu-1A poorly developed.

The wings match those of some species of *Ameropterus* Esben-Petersen, 1922 (e.g., *mexicanus* (van der Weele), *trivialis* (Gerstaecker)), in the overall shape of the FW and venation of both wings. Penny (2002) gives the diagnostic characters for *Ameropterus* as Ma, Mp and Cu in the HW forming a set of three parallel veins angled diagonally across most of the wing. *Ameropterus* is, of course, a split-eyed genus, and one would assume eye shape would have been one of the first attributes Navás checked in making his diagnosis; however, he makes no mention of the shape or entirety of the eyes in his description or in his subsequent treatments (Navás 1912b, 1913).

electrodominicana ***Grimaldi and Engel, 2007†***

incertae sedis within Haplogleniinae **new status**

Amoea electrodominicana† Grimaldi and Engel, 2007

—Engel and Grimaldi 2007.09.06 r#12315: 41, figure 44. {OD: ♂, D, DIS, ET. TS: holotype by original designation. TL: Dominican Republic. TA: Miocene. TR: AMNH. Type specimen not examined (see "Discussion" below).}

Etymology and nomenclatural notes.—*electrodominicana*: electrum (Latin), 'amber' + dominicanus (Latinized adjective), 'Dominican'; a reference to Dominican amber, in which the type specimen was discovered.

Discussion: A careful examination of the figure and description provided by Engel and Grimaldi reveals that *electrodominicana* does not belong within *Amoea*. The specimen exhibits the following features completely uncharacteristic of *Amoea*. Head rather compressed longitudinally and elongate ventrad. Eyes very small. Antennae as long or longer than the FW. Each antennomere with distinct small apical setae. Antennal club distinctly spindle shaped and apically acuminate. Femora and tibia extremely slender, elongate, tarsi relatively short (all possibly an artifact of the illustration). FW Sc+R recurving anterad to strike the wing apex rather far forward, creating a rather broad but short apical area. Apical area with many rows of cells, and marginal row cells separated by veinlets that are branched. FW presectoral area with four cells. FW hind margin slightly concave posterad of Cu fork. HW base relatively narrow, anal area relatively very narrow, cells compressed.

Grimaldi and Engel, who provide an excellent drawing of their specimen but unfortunately no photographs (as for other fossil species in the same paper), state that except for the pterostigmata, the type specimen and *Amoea* lack pigment in the wings that is found in all other Haplogleniinae. However, several species of *Amoea* have pigment in the wings, as demonstrated in the current study: some have the costal and/or subcostal areas lightly tinted, and there are many species that, at least occasionally, express varying degrees of melanism in males and/or females. There are also several Haplogleniinae genera whose species lack pigment in the wings (e.g., *Protidricerus*, *Nicerus*, etc.).

In the very long antennae, narrowed hind wing and hind wing venation, this species is reminiscent of the ascalaphine New World genera *Ameropterus* and *Ascalorphne*, but the entire eyes (whose smallness is very peculiar) indicate this species belongs within Haplogleniinae. Almost no extant Haplogleniinae have been recorded from the Caribbean, although new records of *Ascalobyas* from (the nearly continental) Trinidad and Tobago are presented in this paper (see below), and the type specimen of *Byas microcerus* Rambur, 1842 bears the label “Antilles”.

Genus Neascalobyas *new genus*

Type species *Ascalobyas machadoi* Penny, 1982, by present designation

Etymology.—*Neascalobyas*: neo- (Greek), 'new', + ascalo- (Latinized and truncated form of Askalaphos, Greek), for Greek protagonist Ascalaphus who was cursed and turned into an owl, + byas (Greek), 'a kind of owl', = 'New *Ascalobyas'*. This genus is named for its affinity to *Ascalobyas* Penny. *Gender*: masculine, from the Greek noun byas.

Diagnosis.—Antennae not extending past second fork of Rs in FW of spread specimens. Wings slightly narrower mesally than in *Ascalobyas*; FW with apex subacute and HW with anterior and posterior margins at midpoint parallel, apex slightly expanded and round. Costal margins usually devoid of pigment. Pterostigma veinlets usually dark and membrane pigment hyaline pale brown.

Synapomorphies.—HW anterior and posteror margins of males essentially parallel from Mp_1 to pterostigma, then very slightly and briefly divergent; HW apex shape symmetrical, rounded.

Distribution.—Central America; Amazon River drainage basin.

Description.—

Head. Breadth slightly superequal to width of mesothorax at wing base. Vertex sagittal plates present, concolorous with vertex and sometimes obscure; anterosagittal plate expressed as very slender parasagittal bands posteriorly diverging in a broad curve; posterosagittal plate developed or not, ovoid; vertex setae variable, moderately sparse to very dense. Extra-torular sclerites narrow, fusing mesally. Paraocular band broad, glabrous. Frons broadly and transversely swollen with dense setae. Setosity of mouthparts as in other owlflies (e.g., *Allocormodes*). Eyes entire, dorsally slightly enlarged, in lateral view somewhat dorsoventrally oblong, with a slight dorsoventral mesal depression, more so than in *Ascalobyas*. Antennae flagellomeres with shape undifferentiated; verticils absent; clubs pyriform, covered in fine setae.

Thorax. Pronotum. Anterior flange narrow. Medial transverse band narrow mesally, broadening slightly laterally, posterolateral knob produced, apically bulbous. Posterior flange of females produced somewhat dorsoposteriorly, covering mesoacrotergite, dorsal surface velvety, ventral surface membranous with a dense covering of very fine microsetae, white coating absent; males as in females, except posterior flange more produced, valve-like, overlapping acrotergite and portion of mesoprescutum, laterally bent or not, articulable or not, ventral surface often with coating of white crystalline material. *Pteronotum*. More or less evenly brown to dark brown, finely setose. *Pleuron*. Evenly brown to variegated brown with some yellow, with no hint of a subalar stripe.

Legs. Short, femora and tibiae more or less coequal in length, tarsi slightly subequal. Tibial spurs more or less straight, not reaching past apex of second tarsomere.

Wings. In females intermediately broad, in males somewhat narrower, in both sexes FW mesally broader than HW, and HW base expanded, HW mesal portion with anterior and posterior margins parallel; HW costal area narrowing to a point one-third distance from apex of wing, then broadening again proximad of pterostigma; FW apex subacute, HW apex more round, with a slightly bulbous appearance, particularly in males. *FW*. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal. Pterostigma with four to five forked and unforked dark brown veinlets; membrane more or less pale, translucent to opaque, distal margin of pigment straight. Presectoral area with eight, rarely nine, cells. Anal area hind margin convex, anal angle not developed into a process, a single cell row distad of Cup + 1a, cells undivided by crossveins. Costal and subcostal areas usually devoid of pigment, rarely faintly tinged. Apex of wing devoid of pigment. *HW*. Pre-Mp_1 area posterior margin expansion shorter and rounder in males. Anal area with two rows of cells, marginal row cells undivided by crossveins. Costal and subcostal areas usually devoid of pigment, costal area rarely slightly tinged. Apical one-fourth of wing fuscous or not, pigment sometimes only weakly expressed.

Abdomen. In males long and slender, reaching to pterostigma, or slightly past, when wings folded over the back; in females not reaching to pterostigma. *Tergum*. More or less evenly brown. T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly brown with some small yellow maculations. Some intermediately long, wispy setae on S2 and base of S3. *Pleural membrane*. Devoid of long setae.

Male terminalia. Ectoprocts simple. S9 apical margin obtusely angled. Pulvini small, bearing long slender setae. GPC weakly sclerotized; in lateral view dorsomesally notched; in ventral view intermediately broad. Parameres sclerotized, unproduced, in ventral view appearing like cloven hooves but not curved. Pelta weakly sclerotized, almond-shaped.

Female terminalia. Ectoprocts simple. Ventrovalvae in lateral and ventral views elongate and at least somewhat narrow. Distivalvae in lateral view triangular. Linguella weakly developed. Interdens weakly sclerotized, small, cylindrical, bearing several short slender setae.

Discussion.—When Penny (1982b) described the new species *machadoi* he placed it within *Ascalobyas* on account of its short antennae. It also has darkened hind wing apices similar to Penny's (1982b, 2002) interpretations of *albistigma* Walker and *microcerus* Rambur (the latter two are determined herein to be conspecific). It differs considerably, however, in wing shape, costal area infuscation, pterostigma shape and color, and in several other features. In the cladistic analysis (A3 Fig. 1, node 14), *machadoi* (with new sister-species *nigrantia*) was placed at the base of the largest group of NWHs (this large clade sister being to *Amoea*), immediately outside of *Ascalobyas* + all remaining NWH (node 15). The clade containing *machadoi* is recognized here as a new genus, *Neascalobyas*.

Included species.—*machadoi* Penny; *nigrantia* n. sp.

Key to the species of Neascalobyas

(adult males and females)

1. Legs dull yellowish to amber brown, anterolateral surfaces of femora and tibia dark reddish brown, tarsi dull reddish brown; HW maculation well expressed, brown; males: frons and vertex setae moderately thick, golden yellow to brown, not black [Brazil, Ecuador, French Guiana, Peru, Venezuela] .... ***machadoi*** **Penny**

1’. Trochanters and femora in proximal two-thirds distinctly yellow, femora in apical third and all surfaces of tibia dark brown, tarsi nearly black; HW maculation weakly expressed; males: frons and vertex setae thick, black [Costa Rica, Panama] .... ***nigrantia*** **n. sp.**

Neascalobyas machadoi *(Penny, 1982) new combination*

(A3 Figs. 23–24, 83)

Ascalobyas machadoi Penny 1982b

—Penny 1982b r#5103: 610, fig. 4, map 2 {OD: ♂, BIO, D, GD, ET, FP. TS: not indicated [holotype by explicit monotypy]. TL: “65 km S. W. of Itaituba” (Brazil). TR: INPA. Type specimen not examined (see “Discussion”, below).}

Etymology and nomenclatural notes.—*machadoi;* a Latinized noun in the genitive case (Art. 11.9.1.3), named by Penny for Dr. Prof. Angelo Machado, a Brazilian Odonatist with an interest in Neuroptera.

Diagnosis.—Legs dull yellowish to amber brown; anterolateral surfaces of femora sometimes diffusely, and tibia sometimes sharply, darkening to reddish brown; HW apex maculation usually well expressed, with a sharp proximal margin, brown; males: frons and vertex setae moderately thick, golden yellow to brown, not black.

Autapomorphies.—wing length of males less than 35 mm; tarsi evenly yellowish-red to reddish brown, apex not pale; deltus completely devoid of pigment or pigment very faint.

Distribution.—Amazon River drainage basin: Brazil, Ecuador, French Guiana, Peru, Venezuela.

Description.—

Size (mm). Male: length of body 31–38, abdomen 23–38, forewing 29–35, hind wing 26–32, antennae 13–16. Female: length of body 26–32, abdomen 17–22, forewing 34–38, hind wing 31–33, antennae 14–16.

Head. Size variable, breadth at widest point (of eyes) slightly superequal to width of mesothorax at wing base, smaller (but slightly larger proportionally) in males than in females. Occiput brown. Vertex brown; anterosagittal plates concolorous with vertex, diverging in a broad curve just posterad of high point of vertex, texture granular; posterosagittal plate concolorous with vertex, ca. three times as broad as collective narrow portion of anterosagittal plates, divided by epicranial suture, texture granular; setae, in males, moderately sparse, moderately long, slender, golden, becoming more sparse posterad, females as in males, but somewhat more sparse, quickly transitioning to brown dorsally and posteriorly. Extra-torular sclerites dark brown. Paraocular band dusky dark brown dorsally, transitioning to orangish or dusky yellow ventrally. Frons dusky dark orangish-brown; setae moderately long, slender, golden, sometimes with darker brown tips. Clypeus orange or yellowish, sometimes with a small diffuse dark macula sublaterally, often with a diffuse sagittal brown line distally. Labrum concolorous with clypeus, often with a diffuse sagittal brown line contiguous with that on clypeus. Mandibles dull yellow basally, transitioning to very dark reddish-brown apically. Labium concolorous with labrum. Eyes in anterior view dorsally slightly enlarged, in lateral view somewhat dorsoventrally oblong, with a hint of a dorsoventral mesal division, more so than in *microcerus*. Antennae flagellomeres with internodes brown to dark brown, becoming darker in distal third, nodes narrowly pale; clubs dark brown, anterolateral surface with a short, narrow, diffuse orangish stripe.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, golden setae. Cervical sclerite evenly medium brown. *Pronotum.* Posterior flange of females produced somewhat dorsally, covering mesoacrotergite, white coating absent; males as in females, except posterior flange more produced, valve-like, overlapping acrotergite and most of mesoprescutum, especially laterally, and laterally bent or not, articulable, ventral surface often with coating of white crystalline material. Pronotum coloration more or less evenly brown, in females mesal portion of dorsal surface of posterior flange very dark brown, distal margin and sometimes sagittal region diffusely pale orange or reddish to pale brown, dark portions velvety; in males dorsal surface of posterior flange almost completely very dark brown except with a short, diffuse, reddish sagittal stripe, margin sometimes medium brown, surface velvety. Setae on all surfaces medium to somewhat long, slender, brown. *Pteronotum*. More or less evenly brown, velvety spots of metascutum slightly darker than other surfaces of sclerite; entire surface of pteronotum covered with intermediately dense, intermediately long, slender, golden setae. *Pleuron* in males evenly brown, with no hint of a subalar stripe, setae evenly intermediately dense, intermediately long, very fine, golden; females as in males, but color pattern often variegated yellow and brown, predominately brown.

Legs. Femora and tibiae dull yellow, dorsal and anterolateral surfaces dusky brown. Tarsi dull reddish-brown, tibial spurs and tarsal claws dark reddish-brown. Coxae with intermediately dense, medium length, slender, very pale yellow setae; femora and tibiae with long, stiff, black setae; antennal comb setae somewhat elongate, predominately copper colored, black in distal portion.

Wings. Dimension and shape. Only HW mesal portion with anterior and posterior margins parallel. *Venation/cells.* FW. Pterostigma membrane pale to slightly brownish cream, translucent to opaque. Deltus pigmentless to slightly brownish, translucent to very weakly opaque. Presectoral area with eight cells. Rs with five forks. Mp_2 + Cua_1

evenly and shallowly curving toward hind margin in distal portion. Cubital area with ca. seven to eight irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells . *Color and patterning.* Venation brown to dark brown. Costal and subcostal areas usually devoid of pigment, costal area rarely faintly tinged. Remainder of wing devoid of pigment. HW. As in forewing except as follows. Mp_2 fork angle nearly 90°. Medial triangle distal domain very short, with one cell. Pre-Cup axillary disk brown to dark brown, distal margin broadly paler and often devoid of pigment. Pre-Mp_1 area posterior margin expanded, shorter and rounder in males. *Color and patterning.* Costal and subcostal areas usually devoid of pigment, costal area rarely faintly tinged. Apical one-fourth of wing distinctly translucent brown, pigment sometimes less darkly expressed, occasionally absent.

Abdomen. Tergum. More or less evenly reddish-brown, distal portion of each tergite sometimes with a diffuse, transverse, very narrow black band; T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, golden setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly brown, S3 occasionally with a small diffuse yellow macula in proximal margin, sternites sometimes with diffuse yellowing; mostly devoid of long setae, some intermediately long, wispy, golden setae on S2, base of S3 with a few wispy, golden brown setae. *Pleural membrane*. Devoid of long setae.

Male terminalia. Unmacerated specimens. GPC usually not everted, pulvini not visible. *Macerated specimens.* Ectoprocts simple. S9 apical margin obtusely angled. Pulvini moderately small, ca. three times as long as wide at base, bearing numerous intermediately long, slender, brown setae. GPC weakly sclerotized; in lateral view dorsally slightly arched, dorsomesally notched, ventrally slightly irregular; in ventral view intermediately broad laterally. Parameres sclerotized, in lateral view unproduced, in ventral view simple, appearing like cloven hooves but not curved, proximal margins weakly differentiated. Pelta sagittally with a few microsetae.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distivalvae reddish to dark brown. *Macerated specimens.* Ectoprocts simple. Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. three times width. Distivalvae in lateral view triangular. Linguella membranous, transversely oriented, bilobed, bearing short, stiff, setae. Interdental space triangular, glabrous. Interdens somewhat weakly sclerotized, small, with a round base, short, cylindrical, bearing several short, slender, setae.

Variation. Some males are rather small.

Type material examined.—Not available for this study.

Additional material examined.—*Brazil*: Amazonas (INPA: 5 ♂♂, JRJ_00251, JRJ_00252, JRJ_00253, JRJ_00255, JRJ_00256, 3 ♀♀, JRJ_00257 [A3 Fig. 24], JRJ_00258, JRJ_00259); Rondônia (FSCA: 4 ♂♂, JRJ_00248 [A3 Fig. 23], JRJ_00249, JRJ_00250, JRJ_00254, 2 ♀♀, JRJ_00260, JRJ_00261). *Ecuador*: Pastaza (UMMZ: 1 ♀, JRJ_00272). *French Guiana*: Cayenne (FSCA: 1 ♂, JRJ_00267, 1 ♀, JRJ_00275). *Peru*: Madre de Dios (UDCC: 1 ♂, JRJ_00265, 1 ♀, JRJ_00274; USNM: 2 ♂♂,

JRJ_00263, JRJ_00264, 1 ♀, JRJ_00262). *Venezuela*: Amazonas (USNM: 1 ♂, JRJ_00266).

Morphology, biology and ecology.—Penny reported that the holotype was collected in October, at a light, in a "cutover area of upland forest…within 1 km of the Tapajós River." Label data from project material indicates most individuals were caught at mercury vapor and/or ultraviolet light sources. A few labels give the habitat as "subtropical moist forest".

Discussion.—This species was described from a single specimen collected deep in the Amazon jungle, and has quite distinct wing shape and patterning. The collection localities of the more than twenty specimens made available for this study reveal that the species is widely distributed throughout the Amazon drainage and at a broad range of elevations, from the coast of French Guiana (ca. 50 m) to the foothills of the Andes in Ecuador (>1300 m) and Peru (>350 m). Females are very similar in appearance to those of the new species *nigrantia*, but can be distinguished by the coloration of the legs, wing length, and distribution. Males can be differentiated by the coloration of head setae, leg coloration, size, distribution, and usually wing coloration.

Neascalobyas nigrantia *new species*

(A3 Figs. 25–26, 83)

[*Ascalobyas microcerus* (Rambur, 1842)]

—Penny 2002.10.21 r#10230: 178, fig. 10 {AD, BIO, D, GD, FP, K. All, except GD, based on a misidentification of an undescribed new species, here named *Neascalobyas nigrantia* n. sp.—see "Discussion" below.}

Etymology and nomenclatural notes.—niger (Latin), 'black', + antia (Latin), 'forelock ', = 'black forelock'. Named for the thick shock of black setae on the frons and vertex of males.

Diagnosis.—Trochanters and femora in proximal two-thirds distinctly yellow, femora abruptly in apical third and all surfaces of tibia dark brown, tarsi very dark brown, almost black; HW maculation often very weakly expressed; frons with a small sagittal swelling ventrad of extra-torular sclerites; males: frons and vertex setae thick, black.

Autapomorphies.—frons and vertex setae variable but not dense and dark brown to black; clypeus with a dark dorsolateral maculation; antennal flagellum normal, nodes dark, node apex thinly very pale whitish, base of each flagellomere pale yellowish; pulvini very small and poorly developed, apex with small apical tuft of intermediately long setae.

Distribution.—Costa Rica, Panama.

Description.—

Size (mm). Male: length of body 36–43, abdomen 26–32, forewing 36–41, hind wing 32–36, antennae 17–20. Female: length of body 36–39, abdomen 24–28, forewing 42–43, hind wing 38–39, antennae 16–18.

Head. Size variable, breadth at widest point (of eyes) slightly superequal to width of mesothorax at wing base. Occiput brown. Vertex brown; anterosagittal plate hard to see in males because of setae density, concolorous with vertex, posteriorly diverging in a broad curve, texture granular; posterosagittal plate concolorous with vertex, weakly developed, inconspicuous; setae in males very dense, moderately long, slender, dark brown to almost black from near antennae to dorsum of vertex, becoming more sparse and lighter brown posterad, females as in males, but dark brown only near antennae, quickly transitioning to brown and golden on dorsum of vertex, brown posteriorly. Extra-torular sclerites dark brown. Paraocular band dusky dark yellowish-brown to dark brown. Frons with a small sagittal swelling immediately ventrad of extra-torular sclerites, dusky dark orangish-brown; setae moderately long, slender, in males dark brown, in females golden brown to dark brown. Clypeus yellow mesally, diffusely dark brown laterad. Labrum concolorous with mesal portion of clypeus. Mandibles dull yellow basally, transitioning to very dark reddish-brown apically. Labium concolorous with labrum, with a thin very dark brown sagittal line. Eyes in anterior view dorsally slightly enlarged, in lateral view somewhat dorsoventrally oblong, with a hint of a dorsoventral mesal division, more so than in *microcerus*. Antennae flagellomeres with internodes brown to dark brown, becoming darker in distal half, nodes pale; clubs dark brown, deflated in all pinned specimens.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, dark brown setae. Cervical sclerite evenly medium brown. *Pronotum.* Posterior flange of females produced somewhat dorsally, covering mesoacrotergite and proximal portion of mesoprescutum, ventral surface not visible in available specimens; males as in females, except posterior flange more produced, valve-like, overlapping acrotergite until near midpoint of mesoprescutum, and laterally bent or not, but not articulable, ventral surface interior portion not visible in available specimens, but hint of white coating seen near margin in one or two specimens. Pronotum coloration more or less evenly somewhat dark brown, mesal portion of dorsal surface of posterior flange dark brown, anterior and lateral portions diffusely medium to reddish-brown, mesal surface velvety. In females, setae on all surfaces medium to somewhat long, slender, golden brown to brown; in males dark brown. *Pteronotum*. Evenly brown to dark brown, velvety spots of metascutum concolorous with to slightly darker than other surfaces of sclerite; entire surface of pteronotum covered with intermediately dense, intermediately long, slender, brown setae. *Pleuron* evenly brown, with no hint of variegation or a subalar stripe, setae evenly intermediately dense, intermediately long, very fine, golden to golden brown.

Legs. Femora yellow in proximal two-thirds, dark brown in distal third. Tibia dark brown. Tarsi very dark brown to black, apex of terminal tarsomere narrowly very diffusely dark reddish, tibial spurs and tarsal claws dark reddish-brown. Coxae with intermediately dense, medium length, slender, golden setae; femora and tibiae with long, stiff, black setae; antennal comb setae somewhat elongate, predominately dark golden, black in distal portion.

Wings. Dimension and shape. In both wings mesal portion with anterior and posterior margins parallel. *Venation/cells.* FW. Pterostigma membrane very pale to slightly brownish cream, translucent to opaque. Deltus anteromesally dark brown, otherwise paler, yellowish. Presectoral area with eight, rarely nine, cells. Rs with six branches. Mp_2 + Cua_1 evenly and shallowly curving toward hind margin in distal portion. Cubital area with ca. nine irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells . *Color and patterning.* Venation brown to dark brown. Costal and subcostal areas devoid of pigment, subcostal area sometimes very slightly tinged. Remainder of wing devoid of pigment. HW. As in forewing except as follows. Mp_2 fork angle nearly 90°. Medial triangle distal domain rather short, with one to two cells. Pre-Cup axillary disk brown to dark brown, distal margin paler, often devoid of pigment. Pre-Mp_1 area posterior margin expanded. *Color and patterning.* Costal and subcostal areas devoid of pigment. Apical pigment absent in nearly all specimens, weakly expressed in a single female (JRJ_00271—Fig. 26), but darker pigment may be a more common feature of males and females when more samples are examined (see HW of male in Penny 2002 fig. 10).

Abdomen. Tergum. More or less evenly brown, distal portion of each tergite often with a diffuse, transverse, narrow black band; T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, brown setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly brown, S3 sometimes with a small diffuse yellow macula on proximal margin, mesal sternites sometimes with very faint, very diffuse, yellowing; mostly devoid of long setae, some intermediately long, wispy, golden setae on S2, base of S3 with a few wispy, golden setae. *Pleural membrane*. Devoid of long setae.

Male terminalia. Unmacerated specimens. GPC usually not everted, pulvini not visible. *Macerated specimens.* Ectoprocts simple. S9 apical margin obtusely angled. Pulvini very small, ca. three times as long as wide at base, bearing numerous intermediately long, slender, brown setae. GPC very weakly sclerotized; in lateral view dorsomesally distinctly notched, ventrally more or less entire, mesal portion of dorsal and ventral margins very slightly convergent apicad; in ventral view intermediately broad laterally. Parameres sclerotized, in lateral view unproduced, in ventral view simple, appearing like cloven hooves of a deer but not curved, proximal margins weakly differentiated. Pelta without visible microsetae.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distivalvae reddish to dark brown. *Macerated specimens.* Ectoprocts simple. Ventrovalvae in lateral and ventral views elongate and narrow, length ca. four times width. Distivalvae in lateral view triangular. Linguella small, somewhat weakly developed, weakly bilobed, bearing some short, stiff, setae. Interdental space subtriangular, glabrous. Interdens somewhat weakly sclerotized, small, with a round base, short, cylindrical, bearing several short, slender setae.

Variation. Specimen JRJ_00271 (A3 Fig. 26) with S2 mesally yellow, and S3 and S4 with a broad, diffuse, irregular, yellow sagittal maculation pattern.

Type material examined.—*Holotype* (A3 Fig. 25), **new designation**, male, Panama, in CAS collection: "Panama Chirìqui Hornitos 1000 m 13 V 94 Curoe col /// Amoea vacuus det. Penny, '00 /// HOLOTYPE Neascalobyas nigrantia Jones ♂ design. J. R. Jones 2014 /// JRJ_00269". Condition: Excellent, antennae and wings spread, right front leg missing.

Additional material examined.—*Costa Rica*: Alajuela (CAS: 2 ♂♂, JRJ_00276, JRJ_00277). *Panama*: Chiriqui (CAS: 2 ♂♂, JRJ_00268, JRJ_00270, 1 ♀, JRJ_00271 [A3 Fig. 26]; TAMU: 1 ♀, JRJ_00273).

Morphology, biology and ecology.—One specimen was recorded to have been collected at a light. All were collected at elevations between 850 and 1175 m.

Discussion.—Penny's (2002) treatment of *Ascalobyas microcerus* appears to refer to *nigrantia*. It is very brief and provides a succinct diagnosis (antennae short, FW apex 'pale' [= devoid of pigment], pterostigma dark) but no detailed description of morphology. Clues to the correct identity of the specimens he examined are derived from his illustration (fig. 10). His figure is of a male *nigrantia*; its distinctive wing shape easily identifies it as a male and distinguishes it from *microcerus* Rambur (herein determined to be senior subjective synonym to *albistigma* Walker—see Penny's figure

8). One anomaly concerns the dark maculation at the apex of the HW shown in Penny's figure. In all loan material of *nigrantia* examined here (admittedly few specimens), not one male had the HW with maculation expressed; one female, however, did have the maculation evident but weakly expressed. Brown HW tips were seen in nearly every male of *machadoi* examined, but their range does not appear to extend into Central America. It may be the dark wingtips are a common feature of *nigrantia* males (and that sample size in this study is too small to reveal it), or a regional phenomenon.

Penny (2002) gives the distribution of *microcerus* as from Mexico to Ecuador and Brazil (based on his interpretation of *microcerus* as individuals with the FW lacking apex pigment), but this is likely not correct if interpreted to apply to *nigrantia*, which appears to be an isthmian species. True *microcerus* is vastly Neotropical, occurring from northern Mexico to northern Argentina (see treatment for *Ascalobyas microcerus* (Rambur), below).

Genus* Ascalobyas *Penny, 1982

type species *Byas microcerus* Rambur, 1842, by monotypy

Ascalobyas Penny, 1982

—Penny 1982a r#5105: 395 {TSP: *Byas microcerus* Rambur. TS: holotype by monotypy (of *Byas* Rambur). D, GD, IS, K, NN ("*Ascalobyas*" as objective replacement name for *Byas* Rambur, 1842, preoccupied by *Byas* Dalman in Billberg, 1820 (Lepidoptera) and *Byas* Morris, 1837 (Aves)).}

—Penny 1982b r#5103: 607 {D, DIS, GD, IS, K, SYN, TR, TS}

—Tjeder 1992 r#7246: 36 {BIO, MOR}

—Oswald and Penny 1991.12.02 r#7138: 10 {SYN, TS, TSP}

—Penny et al. 1997.12.09 r#8867: 41 {L}

—Penny 2002.10.21 r#10230: 177 {BIO, D, GD, IS, K}

—Onore et al. 2014.03.30 r#15564:88 {BIO, MOR}

Byas Rambur, 1842

—Rambur 1842.12.31 r# 5314: 361 {TSP: *Byas microcerus* n. sp. TS: not explicitly indicated [holotype by explicit monotypy]. OD, K.}

—Walker 1853 r#6194: 445 {JSYN (of *Ascalaphus* Fabricius), RD}

—Hagen 1866 r#460: 373, 389 {D, IS}

—Brauer 1868 r#1691: 396 {K}

—McLachlan 1871.09.14 r#353: 233 {JSYN (of *Haploglenius*, Burmeister)}

—Taschenberg 1879 r#5954: 217 {K}

—van der Weele 1909.01.05 r#420: 29 {D, DIS, GD, IS, K, RD: ♂♀, TR, TS}

—Navás 1912b.10.31 r#542: 206 {D, IS, K}

—Navás 1913 r#1207: 46 {D, IS, K}

—New 1971 r#4457: 75 {BIO, MOR}

—Henry 1972 r#2875: 2 {BIO, MOR}

—Eisner and Adams 1976.04.20 r#2200: 304 {BIO, MOR}

—Shetlar 1977 r#5727: 83 { Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Haploglenius*)}

—Penny 1978.09.15 r#5098: 11 {IS, L}

—Henry 1978a r#2880: 9 {BIO, EVO, MOR, PHY}

—Henry 1978b r#2878: 75 {BIO, EVO, MOR, PHY}

—Oswald and Penny 1991.12.02 r#7138: 14 {JSYN (of *Ascalobyas* Penny), L}

Etymology.—*Ascalobyas*: ascalo- (Latinized and truncated form of Askalaphos, Greek), for the mythical Greek protagonist who was cursed and turned into an owl, + byas (Greek), 'a kind of owl', = 'Askalaphos owl'. This replacement name was given in reference to the name it replaced, Byas, and to the generic prefix 'Ascalo-', common in the owlflies. *Gender*: masculine, from the noun byas.

Diagnosis.—Antennae not extending past second fork of Rs in FW of spread specimens. Costal margin of FW infuscate, of HW mostly devoid of pigment. Pterostigma veinlets and pigment usually pale yellow. Wings slightly broader than in *Neascalobyas*; HW anterior and posterior margins at midpoint slightly convergent apicad, with apices subacute. FW anal area margin convex with angle unproduced. HW anal are with two complete rows of cells. Thoracic pleuron lacking a pair of oblique broad yellow stripes.

Synapomorphies.—HW pterostigma margined, but not FW.

Distribution.—Widespread: northern Mexico to northern Argentina, with a single record from southern Texas.

Description.—

Head. Large, breadth at widest point (of eyes) wider than mesothorax at wing base. Vertex sagittal plates present, often obscure: anterosagittal plate divided into very narrow parasagittal bands, posteriorly diverging; posterosagittal plate ovoid, only narrowly sagitally divided by epicranial suture. Extra-torular sclerites each a narrow band, mesally fused. Paraocular band broad, glabrous. Setae at least moderately dense on frons and anterior portion of vertex. Setosity of mouthparts as in other owlflies (e.g., *Allocormodes*). Eyes entire, slightly enlarged dorsally, with a hint of a dorsoventral mesal division, but dividing sulcus absent. Antennae flagellomeres with shape undifferentiated; verticils absent; clubs elongate pyriform with only weakly truncated apices, covered in fine setae.

Thorax. Pronotum. Anterior flange narrow, slightly produced dorsad. Medial transverse band very narrow mesally, broadening slightly laterally, posterolateral knob produced, apically bulbous. Posterior flange of females produced somewhat dorsally, covering mesoacrotergite; in males more produced, valve-like, overlapping mesoacrotergite and portion of mesoprescutum, laterally bent but not articulable, mesal surface velvety; ventral surface membranous, membrane contiguous with mesonotal acrotergite, with a dense covering of very fine microsetae, in males often with thick coating of white crystalline material. *Pteronotum*. More or less evenly brown to dark brown. *Pleuron*. With appearance of a weak subalar stripe accentuated by white setae, completely evenly brown, or variegated brown and dark yellow.

Legs. Short, femora and tibiae more or less coequal in length, tarsi slightly subequal. Tibial spurs more or less straight, not reaching past apex of second tarsomere.

Wings. Long, intermediately broad, apically subacute. *FW*. Costal area with subcostal veinlets not inclined. Pterostigma with membrane usually pale yellow, distal margin of pigment straight to weakly crescent shaped, veinlets occasionally margined, particularly in males, sometimes thickly, with pale to dark brown pigment. Presectoral area with eight to nine cells. Anal area hind margin convex; anal angle not developed into a process; a single cell row distad of Cup + 1a, with or without one to two mesal cells of row divided by crossveins. Costal and subcostal areas usually fuscous, pigment sometimes absent in marginal portions of costal cells near wing base. Apical one-fourth to one-third of wing fuscous, pigment often weakly expressed to absent. *HW*. Pre-Mp_1 area margin at least slightly expanded. Anal area with two rows of cells, marginal row sometimes with one to three cells mesally divided by crossveins. Costal and subcostal areas usually devoid of pigment, except usually slightly darkened in several cells proximad of pterostigma. Apical one-fourth to one-third of wing fuscous, pigment often weakly expressed to absent

Abdomen. In males long and slender, reaching to pterostigma when wings folded over the back; in females, often not reaching to pterostigma, usually much shorter and stouter. *Tergum*. More or less evenly brown; T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly brown, mostly devoid of long setae, some intermediately long, wispy setae on S2. *Pleural membrane*. Devoid of long setae.

Male terminalia. Ectoprocts simple. S9 apical margin obtusely angled. Pulvini small, bearing numerous intermediately long, slender setae. GPC weakly sclerotized, dorsally notched or not. Parameres moderately sclerotized, in lateral view unproduced, in ventral view simple, shape like cloven hooves of a deer but not curved. Pelta moderately sclerotized, broadly almond-shaped to ovoid.

Female terminalia. Ectoprocts simple. Ventrovalvae elongate and very narrow. Distivalvae triangular. Linguella poorly developed. Interdens small, sclerotized, nipple- or pin-like.

Discussion.—Prior to this work (Penny 2002), the genus *Ascalobyas* Penny comprised four species: *Byas microcerus* Rambur, *Ascalaphus albistigma* Walker, *Ascalobyas machadoi* Penny, and *Haploglenius dupuyi* Navás. The first two species were described very early in the taxonomic history of New World entire-eyed owlflies and have appeared in some form or another in the works of nearly all early revisers. Considered here to be one species, *microcerus* is widely distributed in North and South America and commonly collected. But, in spite of having rather conspicuous features, its wing pattern and pterostigma color are somewhat variable, and as such it has been redescribed under a not-brief list of synonyms. Based on the results of the cladistic analysis, the scope of the genus is restricted to include just two species: *A. microcerus*, and a new species from Brazil discovered during the course of this project. *Ascalobyas machadoi* is removed and placed in the new genus *Neascalobyas*, and *H. dupuyi* is determined to be a junior synonym of *A. immaculata* (Olivier) and thus is also removed (see taxonomic treatment for *Amoea,* above).

Included species.—*microcerus* (Rambur); *oswaldi* n. sp.

***Key to the species of* Ascalobyas**

(adult males and females)

1. Pleuron with a white tuft of setae on meso- and metanepisternum; pleural pattern variegated, with yellowish spots and white setal tufts giving appearance of a weak subalar stripe; notum with diffuse yellow maculations; males: HW with pre-Mp_1 area margin only slightly expanded; GPC dorsally weakly notched [widespread, Mexico to Argentina] .... ***microcerus* (Rambur)**

1'. Pleuron without tufts on meso- and metanepisternum; pleural pattern variegated but predominately brown to evenly dark brown, without any indication of a subalar stripe; notum without yellow maculations; males: HW with pre-Mp_1 area margin greatly expanded; GPC dorsally distinctly notched [Brazil] .... ***oswaldi* n. sp.**

Ascalobyas microcerus *(Rambur, 1842)*

(A3 Figs. 27–33, 84)

Byas microcerus Rambur, 1842

—Rambur 1842.12.31 r#5314: 362 {OD: sex not indicated [♀]. TS: not indicated [holotype by explicit monotypy]. TL: “Antilles” [on specimen label]. TR: not indicated [MNHN]. Type specimen examined (see “Type material examined”).}

—Hagen 1866 r#460: 389 {L, NS, TL}

—van der Weele 1906 r#404: 227 {DIS, SYN}

—van der Weele 1909.01.05 r#420: 32, fig. 8 {DIS, GD, D, SYN, TL, TR}

—Navás 1912.10.31 r#542: 207 {D, GD}

—Navás 1913 r#1207: 46 {D, GD}

—Shetlar 1977 r#5727: 83 {TSP)}

—Penny 1978.09.15 r#5098: 11 {GD, SYN}

—Penny 1982a r#5105: 395 {TSP (of new genus *Ascalobyas* Penny)}

—Penny 1982b r#5103: 607 {TSP (of *Ascalobyas* Penny)}

—Oswald and Penny 1991.12.02 r#7138: 10 {TSP (of *Ascalobyas* Penny)}

Ascalaphus microcerus (Rambur, 1842)

—Walker 1853 r#6194: 446 {D, GD, NC}

—Hagen 1861.07.?? r#455: 240, 327 {DIS, GD, L}

Haploglenius microcerus (Rambur, 1842)

—McLachlan 1871.09.14 r#353: 235 {DIS, GD, L, NC}

—Shetlar 1977 r#5727: 86 {Ph.D. dissertation, nomenclatural acts invalid: D, DIS, GD, NS, RD: ♂♀, K, SR, SYN, TR}

Ascalobyas microcerus (Rambur, 1842)

—Penny 1982a r#5105: 395 {L, NC, NS}

—Penny 1982b r#5103: 613, fig. 5, map 3 {D, GD, K, RD: ♂♀, SYN, TR}

—Penny 2002.10.21 r#10230: 178, fig. 10 {=*Neascalobyas nigrantia* n. sp. (see above): AD, D, FP, GD [for *nigrantia* n. sp., part, and *albistigma* Walker, part], K}

Ascalaphus albistigma Walker, 1853 **new synonym**

—Walker 1853 r#6194: 452 {OD: sex not indicated [♀—see van der Weele 1909: 31 and Penny 1982b: 610], D. TS: not indicated [holotype by explicit monotypy]. TL: “Honduras”. TR: BMNH. Type specimen not examined (see “Discussion” below).}

—Hagen 1861.07.?? r#455: 239 {GD, RD: sex not indicated}

—Hagen 1866 r#460: 381 {L, SYN}

—Penny 1982b r#5103: 610 {TR}

Haploglenius albistigma (Walker, 1853)

—Hagen 1866 r#460: 406 {GD, L, NC, SYN}

—McLachlan 1871.09.14 r#353: 236 {RD: ♀, TL}

—van der Weele 1906 r#404: 227 {DIS, SYN}

Byas albistigma (Walker, 1853)

—van der Weele 1909.01.05 r#420: 30, figs. 6, 7 {DIS, GD, RD: ♂♀, SYN, TL, TR, TS}

—Navás 1912.10.31 r#542: 207 {“Byas albostigma” [sic]: D, GD}

—Navás 1913 r#1207: 46 {“Byas albostigma” [sic]: D, GD}

—Penny 1978.09.15 r#5098: 11 {GD, SYN}

—Henry 1978a r#2880: 9 {BIO, EVO, MOR, PHY}

Ascalobyas albistigma (Walker, 1853)

—Penny 1982b r#5103: 609, fig. 3, map 1 {D, FP, GD, H, K, NC, RD: ♂♀, SYN, TR, TS}

—Penny et al. 1997.12.09 r#8867: 41 {GD, SYN, TL, TR, TS}

—Penny 2002.10.21 r#10230: 178, fig. 8 {AD, D, FP, GD, H, K}

Ascalaphus leucostigma Walker, 1860

—Walker 1860 r#6195: 195{OD: ♀, D, DIS. TS: not indicated (syntypes: ♀♀—see McLachlan 1871) [a lectotype needs to be designated from syntype material]. TL: "Amazon region". TR: not indicated (BMNH, OXUM—see McLachlan 1871). Type specimens not examined (see "Discussion" below).}

—Hagen 1866 r#460: 384 {JSYN (of *Haploglenius costatus* (Burmeister))}

—van der Weele 1909.01.05 r#420: 32 {JSYN (of *Byas microcerus* Rambur)}

—Shetlar 1977 r#5727: 86 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Haploglenius microcerus* (Rambur))}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Byas microcerus* Rambur)}

—Penny 1982b r#5103: 613 {JSYN (of *Ascalobyas microcerus* (Rambur)), TR, TS}

Haploglenius leucostigma (Walker, 1860)

—McLachlan 1871.09.14 r#353: 235 {NC, RD: ♀, SR, TL}

Haploglenius terminalis McLachlan, 1873

—McLachlan 1871.09.14 r#353: 235 {OD: ♂♀, D. TS: not indicated [syntypes: a lectotype needs to be designated from syntype material]. TL: "Tapajos" (Brazil). TR: BMNH (2 ♂♂—see Penny 1982b); OXUM. Type specimens not examined (see "Discussion" below).}

—Gerstaecker 1885 r#2556: 2 {MOR}

—van der Weele 1909.01.05 r#420: 32 {JSYN (of *Byas microcerus* Rambur), TS}

—Shetlar 1977 r#5727: 87 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Haploglenius microcerus* (Rambur))}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Byas microcerus* Rambur)}

—Penny 1982b r#5103: 609 {JSYN (of *Ascalobyas albistigma* (Walker)), TR, TS}

Haploglenius hilaris Gerstaecker, 1894

—Gerstaecker 1894 r#2559: 96 {OD: ♂, D. TS: not indicated [holotype]. TL: "Chiriqui" (Panama). TR: not indicated (EMAU—see Penny 1982b). Type specimen not examined (see "Discussion" below).}

—van der Weele 1906 r#404: 227 {DIS, JSYN (of "*H. albistigma* Wlk."), TS}

—van der Weele 1909.01.05 r#420: 30, fig. 6 {JSYN [of *Byas albistigma* (Walker), TS]}

—Shetlar 1977 r#5727: 87 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Haploglenius microcerus* (Rambur))}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Byas albistigma* (Walker))}

—Penny 1982b r#5103: 609 {JSYN [of *Ascalobyas albistigma* (Walker), TR, TS]}

Haploglenius fervidus Gerstaecker, 1894

—Gerstaecker 1894 r#2559: 97 {OD: ♂♀ (=♀♀—see van der Weele 1906, 1909, Penny 1982b), D. TS: not indicated [syntypes—a lectotype needs to be designated from syntype material]. TL: "British Honduras" (Belize). TR: not indicated (EMAU, 2 ♀♀—see Penny 1982b). Type specimens not examined (see "Discussion" below).}

—van der Weele 1906 r#404: 227 {DIS, JSYN (of "*H. albistigma* Wlk."), TS}

—van der Weele 1909.01.05 r#420: 30 {DIS, JSYN (of *Byas albistigma* (Walker)).}

—Shetlar 1977 r#5727: 87 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Haploglenius microcerus* (Rambur))}

—Penny 1978.09.15 r#5098: 11 {JSYN (of *Byas albistigma* (Walker))}

—Penny 1982b r#5103: 609 {JSYN (of *Ascalobyas albistigma* (Walker)), TR, TS}

Haploglenius camposi Navás, 1929

—Navás 1929.02.?? r#860: 107, fig. 16 {OD: ♀, D, DIS, ET. TS: not indicated (syntypes; lectotype ♀ designated by LeGrand (1991)). TL: "Ecuador: Guayaquil, Posorja". TR: not indicated [MNHN, 1♂, 1♀]. Type specimens examined (see "Type material examined" below).}

—Penny 1978.09.15 r#5098: 12 {GD, L}

—Penny 1982b r#5103: 609, 613 {JSYN [♀ syntype, of *Ascalobyas albistigma* (Walker); ♂ syntype of *Ascalobyas microcerus* (Rambur)], TR, TS}

Etymology and nomenclatural notes.—*microcerus*: micro (Greek), 'small, little' + cerus (Latinized and abbreviated form of keras, Greek), 'horn', = "small horn". Although not stated explicitly by Rambur, this species is evidently named for its relatively short antennae.

Diagnosis.—Pleuron with a white tuft of setae on meso- and metanepisternum. Pleural pattern variegated, with yellowish spots and white setal tufts giving appearance of a weak subalar stripe. Notum with diffuse yellow maculations. Pterostigma milky white to reddish yellow. Apical one-fourth to one-third of wings often tinted brown, tinting of FW sometimes fainter, or pigment of both wings faint or altogether absent. Males: HW with pre-Mp_1 area margin only slightly expanded; GPC dorsally weakly notched.

Autapomorphies.—subalar setae forming a thick white coat along subalar stripe; pelta simple, unproduced, faintly sclerotized, broadly almond-shaped.

Distribution.—Widespread: Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Peru, Trinidad and Tobago, U.S.: Texas: Val Verde Co. (probably an incidental record), Venezuela.

Description.—

Size (mm). Male: length of body 35–42, abdomen 26–30, forewing 32–39, hind wing 30–37, antennae 17–19. Female: length of body 31–38, abdomen 22–26, forewing 40–44, hind wing 37–41, antennae 16–20.

Head. Large, breadth at widest point wider than mesothorax at wing base. Occiput brown with some diffuse yellow markings. Vertex medium to dark brown; anterosagittal plate often hard to see, but when well expressed slightly paler brown, narrow, posterior bifurcations splayed laterally at nearly a 90° angle; posterosagittal plate also often hard to see, coequal to or narrower than anterior portion of anterior plate; setae rather dense near antennae, becoming more sparse posteriorly, intermediately long, golden brown near antennae, gradually transitioning to medium brown posteriorly. Extra-torular sclerites dark brown. Paraocular band more or less concolorous with frons and clypeus. Frons medium dusky yellow; setae intermediately dense, amber-colored, becoming browner at tips. Clypeus yellow, a reddish-brown sagittal line sometimes present, each dorsolateral corner sometimes with a large very diffuse brownish macula. Labrum concolorous with clypeus, reddish-brown sagittal line sometimes present. Mandibles dull dark yellow basally, transitioning to very dark reddish-brown apically. Labium concolorous with labrum, with a thin brown sagittal line. Eyes in anterior view dorsally slightly enlarged, in lateral view somewhat dorsoventrally oblong, with a hint of a dorsoventral mesal division. Antennae flagellum mesally pale yellow to medium brown; clubs medium to dark brown, often paler on anterodistal face.

Thorax. Cervix. Dorsal cervical plate setae golden. Cervical sclerite evenly medium brown. *Pronotum.* Posterior flange of females produced somewhat dorsally, covering meso-acrotergite, internal membrane without white coating, in males more produced, valve-like, overlapping acrotergite until midpoint of mesoprescutum, and laterally bent but not articulable, ventral membrane surface often with thick coating of white crystalline material. Pronotum coloration in females more or less evenly medium to somewhat dark brown, except for laterally on medial transverse band and posterior flange, where posterior surface of posterolateral knob and anterior surface of lateral portions of posterior flange yellow; in males, pattern as in females except anterior flange mesally somewhat darkened and dorsal surface of posterior flange dark brown, diffusely slightly paler laterad, mesal surface velvety. In females, all surfaces with medium to somewhat long, slender, golden brown to brown setae; males as in females but long setae becoming very sparse on mesodorsal surface of valve. *Pteronotum*. More or less evenly brown to dark brown, anterior surface of posterior transverse swelling of meso- and metascutellum with a dull yellow to pale brown transverse stripe, but this often very diffuse or weakly expressed; velvety spots of metascutum only slightly darker than other surfaces of sclerite; entire surface of pteronotum covered with intermediately dense, intermediately long, slender, golden brown setae, hind margin of meso- and metascutellum with setae aggregated into a fringe, this not particularly dense but conspicuous because of golden color of the setae. *Pleuron* pattern variegated brown and yellow, predominately brown, posterior surfaces of mes- and metanepisternites with largest blotches of yellow, these bearing a moderately dense patch of intermediately long white setae directed posterad, yellow blotches and white setae collectively giving appearance of a weak subalar stripe, especially when viewed from a distance (not under microscope). Setae otherwise intermediately dense, intermediately long, very fine, dull golden brown.

Legs. Pro- and mesothoracic femora dusky brown, metathoracic femur mostly yellow, distal third of dorsal surface sometimes slightly darkened. Tibia yellow, anterolateral surfaces sometimes slightly darkened and brownish. Tibial spurs more or less straight, not reaching past apex of second tarsomere. Tarsi very dark brown to black, apex of terminal tarsomere diffusely reddish, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, white setae; femora and tibiae with long, stiff, black setae; antennal comb setae predominately golden, black along anterolateral margin.

Wings. FW. Venation/cells. Costal area cells with width and height more or less coequal. Pterostigma with 4-6 mostly unforked pale yellow to dull brown veinlets; membrane usually pale yellow, sometimes darkening to dull pinkish brown, often opaque, distal margin of pigment straight to weakly crescent shaped, slightly produced along margin and with a small portion of pigment produced along Sc + R one to two cell widths; veins occasionally margined, particularly in males, sometimes thickly, with pale to dark brown pigment. Presectoral area with eight to nine cells. Rs with six to seven forks. Mp_2 + Cua_1 evenly curving toward hind margin in distal portion. Cubital area with ca. eight to ten irregular but more or less complete rows of cells. Cubital triangle distal domain with one to three, usually two, cells . Anal area cell row rarely with one or two mesal cells of row divided by crossveins. *Color and patterning.* Venation pale to moderately dark brown, usually medium brown. Costal and subcostal areas usually fuscous, pigment sometimes absent in marginal portions of costal cells near wing base. Apical one-fourth to one-third of wing fuscous, proximal margin of pigment diffuse, pigment often weakly expressed to absent. *HW. Venation/cells.* As in forewing except as follows. Mp_2 fork angle nearly 90°. Medial triangle distal domain rather short with one to two cells. Pre-Mp_1 area margin only slightly expanded. Anal area with two rows of cells, marginal row sometimes with one to two cells mesally divided by crossveins.

Color and patterning. Costal and subcostal areas usually devoid of pigment, except usually slightly darkened in several cells proximad of pterostigma. Apical pigment more commonly present and slightly darker than in FW, but sometimes faint to absent.

Abdomen. Tergum. More or less evenly brown, distal portion of each tergite often with a diffuse, transverse, narrow black band; T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, golden setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly brown, sometimes faintly and diffusely yellow in proximal half; mostly devoid of long setae, some intermediately long, wispy, golden setae on S2. *Pleural membrane*. Devoid of long setae.

Male terminalia. Unmacerated specimens. GPC usually not everted, pulvini not visible. *Macerated specimens.* Ectoprocts simple. S9 apical margin obtusely angled. Pulvini small, ca. twice as long as broad at base, bearing numerous intermediately long, slender, brown setae. GPC weakly sclerotized; in lateral view dorsally more or less entire, basomesally weakly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view somewhat narrow laterally. Parameres moderately sclerotized, in lateral view unproduced, in ventral view simple, appearing like cloven hooves of a deer but not curved. Pelta moderately sclerotized, broadly almond-shaped to ovoid.

Female terminalia. Unmacerated specimens. Ventrovalvae dark brown, distovalvae orangish or light brownish. *Macerated specimens.* Ectoprocts simple. Ventrovalvae in lateral and ventral views elongate and very narrow, length six to seven times width. Distivalvae in lateral view triangular. Linguella small, poorly developed, transversely weakly bilobed, bearing a few short, stiff, setae. Interdental space more or less round, glabrous. Interdens well sclerotized, small, with a round base, short, cylindrical, nipple- or pin-like.

Variation. Antennomeres of some specimens weakly annulated. Pteronotum of some specimens with diffuse parasagittal stripes. Several specimens, including females, with entire wing membranes bearing a very faint brownish tinge, but this not distinctly melanistic.

Type material examined.—*Holotype* of *Byas microcerus* Rambur (A3 Fig. 31), female, "Les Antilles", in MNHN collection: "Antilles Maugé /// Byas microcerus Ramb. /// MUSEUM PARIS Antilles Maugé /// Byas microcerus Rambur Type /// Byas microcerus Rb type de l'__ [illegible] /// TYPE /// 1. /// JRJ_01217". Condition: poor; antennae and wings spread; left antennal club, all legs except left front femur and left middle femur, metathorax, both HWs and abdomen missing, FWs very tattered. *Notes*: Maugé is probably René Maugé de Cely, the French zoologist who worked in the Antilles in 1799. *Lectotype* of *Haploglenius camposi* Navás (A3 Fig. 33), female, Ecuador, in MNHN collection: "Guayaquil (Ecuador) leg. Campos /// MUSEUM PARIS LONGIN NAVÁS LEGIT 19 /// Haploglenius Camposi Nav. P. Navás S. J. det. /// Typus [handwritten] /// LECTOTYPE /// Haploglenius camposi Navás 1988 Lectotype ♀ J. Legrand dét. 8.1991 /// JRJ_01221". Condition: poor; spread; specimen broken and pieced together with glue, head missing, right FW tattered, left HW and antennae broken but still with specimen, legs missing. *Syntype* of *Haploglenius camposi* Navás (A3 Fig.

29), male, Honduras, in MNHN collection: "Guayaquil 1.1930 Campos leg. /// MUSEUM PARIS LONGIN NAVÁS LEGIT. 19 /// Haploglenius camposi ♂ Nav. P.Navás S. J. det. /// Cotypus (handwritten) /// JRJ_01223". Condition: fair; spread; entire body broken and pieced back together with glue, right mesothoracic leg missing, right FW tip broken but glued on, abdomen apex missing.

Additional material examined.—*Brazil*: Bahia (MFNB: 3 ♂♂, JRJ_01845, JRJ_01846, JRJ_01847, 1 ♀, JRJ_01848). *Colombia*: Magdelena (CMNH: 2 ♂♂, JRJ_00385 [A3 Fig. 27], JRJ_00386, 3 ♀♀, JRJ_00387, JRJ_00388, JRJ_00389). *Ecuador*: locality unknown (MFNB: 1 ♂, JRJ_01844). *El Salvador*: La Libertad (FSCA: 1 ♂, JRJ_00329, 1 ♀, JRJ_00331 [A3 Fig. 28]; SDMC: 1 ♂, JRJ_00330). *Guatemala*: El Progreso (JRJC: 1 ♀, JRJ_10215); Peten (TAMU: 1 ♂, JRJ_00328); locality unknown (MFNB: 2 ♀♀, JRJ_01849 [A3 Fig. 32], JRJ_01850; SDEI: 1 ♀, JRJ_01851; UMMZ: 2 ♂♂, JRJ_00332, JRJ_00335, 2 ♀♀, JRJ_00338, JRJ_00339). *Guyana*: Upper Takutu-Upper Essequibo (USNM: 2 ♀♀, JRJ_00397, JRJ_00398). *Honduras*: Francisco Morazan (FSCA: 1 ♂, JRJ_00333); Olancho (BYUC: 1 ♀, JRJ_00336). *Mexico*: Chiapas (TAMU: 1 ♀, JRJ_00308); Guerrero (SDMC: 2 ♂♂, JRJ_00322, JRJ_00323, 4 ♀♀, JRJ_00324, JRJ_00325, JRJ_00326, JRJ_00327,); Jalisco (EMEC: 4 ♂♂, JRJ_00282, JRJ_00283, JRJ_00292, JRJ_00301, 2 ♀♀, JRJ_00305, JRJ_00306); Nuevo Leon (SEMC: 2 ♂♂, JRJ_00279, JRJ_00280; TAMU: 1 ♂, JRJ_00284); Oaxaca (SDMC: 2 ♂♂, JRJ_00285, JRJ_00289; USNM: 1 ♂, JRJ_00299); Quinatana Roo (FSCA: 2 ♂♂, JRJ_00291, JRJ_00296, 8 ♀♀, JRJ_00307, JRJ_00309, JRJ_00310, JRJ_00314,

JRJ_00315, JRJ_00317, JRJ_00319, JRJ_00320; TAMU: 2 ♂♂, JRJ_00293, JRJ_00294); San Luis Potosi (FSCA: 1 ♀, JRJ_00312); Sinaloa (SDMC: 3 ♂♂, JRJ_00288, JRJ_00290, JRJ_00303); Veracruz (BYUC: 1 ♂, JRJ_00304; SDEI: 1 ♀, JRJ_00313; TAMU: 2 ♂♂, JRJ_00286, JRJ_00287); Yucatan (EMEC: 3 ♂♂, JRJ_00298, JRJ_00300, JRJ_00302; FSCA: 1 ♂, JRJ_00295, 4 ♀♀, JRJ_00311, JRJ_00316, JRJ_00318, JRJ_00321; TAMU: 2 ♂♂, JRJ_00281, JRJ_00297). *Nicaragua*: Granada (EMEC: 1 ♂, JRJ_00421, 2 ♀♀, JRJ_00422, JRJ_00423; TAMU: 1 ♂, JRJ_00420). *Panama*: Chiriqui (INPA: 1 ♀, JRJ_00373); Colon (SEMC: 3 ♂♂, JRJ_00343, JRJ_00416, JRJ_00418, 2 ♀♀, JRJ_00362, JRJ_00371; UCDC: 1 ♂, JRJ_00347); Kuna de Madugandi (SDMC: 2 ♂♂, JRJ_00348, 2 ♀♀, JRJ_00355, JRJ_00360); Panama (BYUC: 1 ♂, JRJ_00340, 3 ♀♀, JRJ_00369, JRJ_00375, JRJ_00377 [A3 Fig. 30]; CMNH: 1 ♀, JRJ_00376; EMUS: 1 ♂, JRJ_00342; FSCA: 1 ♂, JRJ_00417, 4 ♀♀, JRJ_00356, JRJ_00359, JRJ_00370, JRJ_00374; SDMC: 1 ♂, JRJ_00351; SEMC: 1 ♀, JRJ_00379; TAMU: 1 ♂, JRJ_00350; UCDC: 4 ♂♂, JRJ_00345, JRJ_00346, JRJ_00349, JRJ_00354, 11 ♀♀, JRJ_00357, JRJ_00358, JRJ_00361, JRJ_00363, JRJ_00364, JRJ_00365, JRJ_00366, JRJ_00367, JRJ_00368, JRJ_00372, JRJ_00378; UMMZ: 2 ♂♂, JRJ_00344, JRJ_00352; UMSP: 1 ♂, JRJ_00341). *Trinidad and Tobago*: Tunapuna-Piarco (FSCA: 1 ♂, JRJ_00381, 2 ♀♀, JRJ_00383, JRJ_00384; USNM: 1 ♂, JRJ_00380, 1 ♀, JRJ_00382). *USA*: Texas (TAMU: 1 ♀, JRJ_00278). *Venezuela*: Táchira (UMMZ: 1 ♀, JRJ_00395); Zulia (FSCA: 1 ♂, JRJ_00396). *Country unknown*: (EMEC: 1 ♀, JRJ_00337).

Morphology, biology and ecology.—Adults of this species are commonly collected at lights in and near forests. From label data, specimens were collected at MV and UV lights in Brazil, Guatemala, Honduras, Mexico, Nicaragua, Panama and Trinidad, in transition forest in Bolivia, and in premontane moist forest in Peru. Penny (1982b) reported a specimen from the INPA campus in Manaus, Brazil, which is secondary forest. Collection site elevations range from ca. 50 m to more than 1400 m.

New (1971) described the eggs, repagula and ovarioles and provided information on clutch size and egg development times of an unidentified species of *Byas* collected at light and on vegetation in central Brazil. However, a few of the details he provided (egg length, egg color, development time) differ from those later described by Henry (1978a) for *Byas albistigma* material from Panama, and it is possible that New had *A. oswaldi* or some other haplogleniine species (perhaps in *Haploglenius*).

Henry (1978a) described the morphology of the eggs, repagula, and larval instars of *microcerus* (as "*Byas albistigma*") reared from a clutch laid by a female captured in Panama, and presented a host of corresponding information on the biology of the various life stages, as follows. Eggs, which are among the largest measured for ascalaphids and operculate as in other species, are orangish yellow when freshly laid, but darken to brownish yellow; under laboratory conditions they developed in 15 days. Embryonic development (as visible externally) and eclosion occur as in *Haploglenius juvenilis* (McLachlan) (as "*Ascaloptynx furciger*") and *Ululodes mexicanus* (McLachlan) (Henry

1972, 1976). Larvae do not litter their dorsum with sand or debris, and when given objects to climb choose to rest on elevated substrates. From these observations and those of colleagues in the field, Henry suggested that larvae are arboreal, "living on the upper sides of aging green leaves on relatively low (1–2 m), recent second growth herbage". Wild specimens are sometimes greenish, and such color may derive from the ingestion of carotenoids present in phytophagous prey (Chapman 1969). Prey capture, paralysis, handling and grooming are as in *H. juvenilis* and *U. mexicanus*, but *microcerus* may take smaller prey. Like *H. juvenilis*, the mandibles are held open at 180°. Larvae fully mature in 5 months and generation time is probably a year or less. The flight period of adult males appears to precede that of females. Natural oviposition sites are unknown.

Discussion.—The taxonomic concept of *microcerus* has presented an enigma to researchers—most of whom appear to not have had access to the holotype—since the publication of Rambur's original description. Hagen (1861) thought *microcerus* might be conspecific with *Ascalaphus costatus* Burmeister but did not synonymize it. McLachlan (1871) could match Rambur's description to no specimen he had seen and made no attempt to redescribe it. Several authors (Rambur 1842, Hagen 1866, Brauer 1868, Taschenberg 1879) left it alone in its own genus *Byas*, refusing to place it with similar species in *Ascalaphus* or *Haploglenius*. Van der Weele (1906) was the first to suggest a close (possibly conspecific) relationship with *albistigma* Walker, and soon after (1909) paired the two within *Byas* and redescribed them. Penny later (1982b, 2002) followed van der Weele (1909) in treating *microcerus* as a sister species to *albistigma* under his new replacement name *Ascalobyas*, but his initial (1982b) interpretation was of a species having yellowish brown pterostigmata and the FW costal margin darkened, while his subsequent characterization (2002) was of a species having dark pterostigma (and the costal area unmentioned, but shown as clear in his figure).

Ascalaphus albistigma Walker has been slightly more well-understood, and authors (McLachlan 1871; van der Weele 1906, 1909; Penny 1982b) have been better able to identify synonyms of it. Penny's (1982b, 2002) keys and diagnoses, in particular, have enabled large numbers of specimens in world collections (based on material made available for this study) to be identified as *albistigma*. Very few haplogleniine specimens, on the other hand, have been observed to bear identification as *microcerus*.

Rambur's *microcerus* holotype was made available for this study. Though the specimen has not fared well over time (Van der Weele 1909 reported a similar condition when he viewed the type over a century ago), the head and eyes, antennae, a portion of the thorax, the leading edges of the FWs, and the pterostigmata are all intact enough to interpret. Examination reveals a large female (based on wing shape and specimen size) with weakly expressed wing maculation, whose appearance (large head and eyes, short antennae, variegated pleuron, mesanepisternite with long setae, FW anal area margin convex) matches what has been labeled as *albistigma* in loan material, as well as Walker's (1853) original description of *albistigma* (short antennae, subalar stripe, unique apical wing maculation).

Penny (1982b, 2002), who reviewed the species most recently, separated *microcerus* and *albistigma* on the basis of the coloration of the forewing apex, that of *microcerus* being (usually) clear and of *albistigma* being dark. He also included a few other differences; he stated that the pterostigma of *albistigma* is white, whereas that of *microcerus* is yellowish brown (1982b) or dark (2002); and he said the antennae of *albistigma* are uniformally pale fuscous, but that in *microcerus* they transition through several colors: reddish brown basally to pale yellow distally, with the club black at the base and yellow at the apex. Examination of large numbers of specimens in this study reveals that these features correspond to a single highly variable species. In this species, the expression of maculation in the distal part of both wings varies in both males and females, exhibiting many intermediate conditions, but these differences do not consistently correspond with variation of other anatomical features, nor with geographic distribution [Penny's (1982b) distribution maps of a handful of specimens suggest that *microcerus* is more coastal, while *albistigma* is central Amazonian and Central American]. Some specimens have very dark wing apices, whereas other essentially identical specimens have the wing maculation only moderately dark, or faint, or even completely absent. Variation in patterning across geographic regions was predicted by van der Weele (1909), who also chose to keep the species separate. He stated that he did not have access to specimens from intermediate areas separating eastern and western forms and thus could not yet confirm the synonymy of the two species; nevertheless he inferred that with more specimens a gradient of transitional forms would be seen and synonymy might be demonstrated. He also asserted that darker wing coloring corresponded in some degree to maturity of specimens. However, outside of teneral specimens having virtually no coloration in the wings, this does not seem to be true, at least in this species. Some very fresh looking specimens have the apical infuscation quite dark, while some rather tattered ones lack wing pigment; both the pterostigma and the antennae color also vary more or less evenly across the samples.

The type specimens of several of the synonyms listed above were not available for this study but were examined by Van der Weele (1906, 1909) and Penny (1982b). Van der Weele (1906) examined the types of *Haploglenius hilaris* Gerstaecker and *Haploglenius* *fervidus* Gerstaecker and considered them synonyms of *albistigma* and possibly *microcerus*. Gerstaecker's description of *hilaris* agrees very well with *microcerus* and *albistigma* (short antennae, pleuron with a yellowish subalar stripe, FW costal area dark and HW costal area not, pterostigma white, HW wing apex pale infuscate); his description of *fervidus* also agrees well, and only differs in the color of the pterostigma, which he describes as 'reddish' (but van der Weele (1909) considered the color description a mistake, although he did not say what color he thought instead it was). Penny (1982b) accepted Van der Weele's synonymies for *hilaris* and *fervidus*. Both van der Weele (1909) and Penny (1982b) examined *Haploglenius leucostigma* Walker and *Haploglenius terminalis* McLachlan. Penny followed van der Weele in regardering *leucostigma* as a synonym of *microcerus* and *terminalis* as a synonym of *albistigma*. The original descriptions of *leucostigma* and *terminalis* correspond to *microcerus*, and are interpreted here to be junior synonyms thereof.

Ascalobyas microcerus is probably the most widely distributed entire-eyed owfly species in the Western Hemisphere, occurring throughout North, Central and South America. The type specimen of *Byas microcerus* bears the label “Antilles”, and this non-specific Caribbean origin was likely an additional contributor to the historical ambiguity of the taxon. The only recent records of *microcerus* or any of its synonyms from any part of the Antilles are from Trinidad and Tobago (material in this study; see also van der Weele 1909 and Penny 2002), which, though considered to be part of the Lesser Antilles, sit very close (<20 km at the nearest point) to the coast of Venezuela. No recent specimens of entire-eyed owlflies have been recorded from the Greater Antilles.

Ascalobyas oswaldi *new species*

(A3 Fig. 34, 84)

Etymology and nomenclatural notes.—*oswaldi:* a Latinized noun in the genitive case. Named for John Oswald, neuropterologist and mentor.

Diagnosis.—Pleural pattern variegated and predominately brown to completely and evenly dark brown, without any indication of a subalar stripe. Meso- and metanepisternum without tufts of white setae. Notum without diffuse yellow maculations. Apical one-fourth to one-third of wings often tinted brown, tinting of HW usually fainter, or pigment of both wings faint or altogether absent. Males: HW with pre-Mp_1 area margin greatly expanded; GPC dorsally distinctly notched Females: Unknown.

Autapomorphies.—antennal flagellum normal, nodes dark, node apex thinly very pale whitish, apex of each flagellomere pale yellowish; basal cell of HW costal area opaque over entire surface, but clear or milky to yellow to pale brown.

Distribution.—Brazil.

Description.—

Size (mm). Male: length of body 39–41, abdomen 28–30, forewing 39–42, hind wing 34–38, antennae 18–21.

Head. Large, breadth at widest point (of eyes) slightly wider than mesothorax at wing base. Occiput brown with a few very small yellow markings at the lateral margin. Vertex dark brown; anterosagittal plates hard to see, concolorous with vertex, posteriorly diverging at nearly a 90° angle, texture granular; posterosagittal plate also hard to see, twice as wide as anterior portion of anterior plate, texture granular; setae rather dense near antennae, becoming more sparse dorsally, intermediately long, very pale brown with dark brown tips near antennae, transitioning to dark brown dorsally and posteriorly. Extra-torular sclerites pale or dark brown. Paraocular band brownish, becoming pale brown to yellow near orbital sclerite. Frons medium dusky orangish-brown; setae intermediately dense, very slender, dark brown. Clypeus dull yellow mesally, slightly darker laterad. Labrum concolorous with mesal portion of clypeus. Mandibles dull dark yellow basally, transitioning to very dark reddish-brown apically. Labium concolorous with labrum, proximal portion with a thin very dark brown sagittal line. Eyes in anterior view dorsally slightly enlarged, in lateral view somewhat dorsoventrally oblong, with a hint of a dorsoventral mesal division. Antennae flagellomeres with internodes dark brown, nodes paler; clubs brown, very slightly paler on anterodistal face.

Thorax. Cervix. Dorsal cervical plates bearing long, slender, golden brown setae. Cervical sclerite evenly dark brown. *Pronotum.* Posterior flange produced, valve-like, overlapping acrotergite until midpoint of mesoprescutum, and laterally bent but not articulable, ventral surface bearing a coating of white crystalline material. Pronotum coloration evenly dark brown, surface velvety. All surfaces with somewhat long, slender, brown setae. *Pteronotum*. Evenly brown to dark brown, velvety spots of metascutum darker than other surfaces of sclerite; entire surface of pteronotum covered with intermediately dense, intermediately long, slender, brown setae. *Pleuron* often completely evenly brown, sometimes variegated brown and dark yellow, with no hint of a subalar stripe, Setae more or less evenly intermediately dense, intermediately long, very fine, dark golden brown.

Legs. Femora and tibiae dull yellow, dorsal and anterolateral surfaces dusky brown. Tarsi very dark brown to black, apex of terminal tarsomere diffusely reddish, tibial spurs and tarsal claws reddish-brown. Coxae with intermediately dense, medium length, slender, white setae; femora and tibiae with long, stiff, black setae; antennal comb setae predominately golden, black along anterolateral margin.

Wings. Dimension and shape. Intermediately broad, HW basiposterior margin more broadly expanded than in *microcerus*, both wings apically subacute. *Venation/cells*. FW. Costal area with width of many cells narrow, particularly in proximal half of wing, one-half that of height. Pterostigma with five to seven mostly unforked pale yellow veinlets; membrane pale to dusky yellow, often opaque, distal margin of pigment essentially straight, with a small portion of pigment faintly produced along Sc + R one cell width. Presectoral area with eight to nine cells. Rs with six to seven forks. Mp_2 + Cua_1 evenly curving toward hind margin in distal portion. Cubital area with ca. eight to eleven irregular but more or less complete rows of cells. Cubital triangle distal domain with one to three, usually two, cells . Anal area cell row with one to three mesal cells divided by crossveins. *Color and patterning.* Venation brown to dark brown. Costal and subcostal areas darkly fuscous, pigment narrowly absent in marginal portions of costal cells near wing base. Apical one-fourth of wing fuscous. HW. As in forewing except as follows. Mp_2 fork angle nearly 90°. Medial triangle distal domain moderately short with two to three cells. Pre-Mp_1 area margin expanded. Anal area with two rows of cells, marginal row with two to three cells mesally divided by crossveins. *Color and patterning.* Costal and subcostal areas devoid of pigment, except slightly darkened in several cells proximad of pterostigma. Apex pigment fainter than in FW.

Abdomen. Tergum. More or less evenly brown, distal portion of each tergite often with a diffuse, transverse, narrow black band; T1 and proximal portions of T2 with intermediately dense, intermediately long, wispy, golden brown setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly brown to dark brown; mostly devoid of long setae, some wispy, golden brown setae on S2. *Pleural membrane*. Devoid of long setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible. *Macerated specimens.* Ectoprocts simple. S9 apical margin obtusely angled. Pulvini small, ca. twice as long as broad at base, bearing numerous intermediately long, slender, brown setae. GPC weakly sclerotized; in lateral view dorsomesally distinctly notched, ventrally more or less entire, mesal portion of dorsal and ventral margins subparallel; in ventral view broad laterally. Parameres moderately sclerotized, in lateral view unproduced, in ventral view simple, shape like cloven hooves of a deer but not curved, lateral margins weakly differentiated. Pelta weakly sclerotized, broadly almond-shaped to ovoid.

Variation. Some specimens are slightly paler overall. One specimen with FW pterostigma veinlets thickly margined with opaque yellow, HW veinlets thickly margined with dark brown (JRJ_00390). One specimen with apical pigment patches very faint in both wings (JRJ_00394).

Type material examined.—*Holotype* (A3 Fig. 34), **new designation**, male, Brazil, in INPA collection: "Brasil, AM Presidente Figueiredo, Am-240, Km 24 02 35 21 S / 60 06 55 W 11-12 /XII/ 2004 F.F. Xavier F; G. M. Lourido /// Armadilha de Luz Mista /// HOLOTYPE Ascalobyas oswaldi Jones ♂ design. J. R. Jones 2014 /// JRJ_00390". Condition: Excellent, wings spread, antennae pulled back, right middle leg missing.

Additional material examined.—*Brazil*: Amazonas (INPA: 2 ♂♂, JRJ_00391, JRJ_00393); Rondônia (MSUC: 1 ♂, JRJ_00394); São Paulo (UMSP: 1 ♂, JRJ_00392).

Morphology, biology and ecology.—Adult specimens were collected at elevations of 80 to 600 m. Two were collected at mercury vapor and black lights. The larvae are unknown.

Discussion.—At first glance this species resembles a darker form of *microcerus*, but its diagnostic characteristics, though subtle, appear reliable; these includes the genitalia, which show several unique differences (GPC with a distinct deep dorsal notch, greater width in ventral view, etc.). Although only a few specimens were discovered in loan material, they come from widely separated locales, and the species appears to have a rather broad distribution within Brazil (as opposed to many new species discovered during this project which have very narrow distributions). It is possible that some specimens of *microcerus* (or *albistigma*, as it was interpreted taxonomically for most of the history of the species) examined by early authors were in fact this species.

Genus* Haploglenius *Burmeister, 1839

Type species *Ascalaphus costatus* Burmeister, 1839, by subsequent designation

Haploglenius Burmeister, 1839

—Burmeister 1839 r#1771: 1000 {TSP: not indicated. TS: not indicated. D, DIS, IS.}

—Lefèbvre 1842.04.?? r#3666: 8 {DIS}

—Rambur 1842.12.31 r#5314: 362 {DIS, RD: ♂, SYN}

—Blanchard 1845 r#7597: 475 {TSP: *Ascalaphus appendiculatus* Fabricius (incorrect, species not included in original genus—see Oswald and Penny 1991)}

—Walker 1853 r#6194: 446 {JSYN (of *Ascalaphus* Fabricius).}

—Hagen 1866 r#460: 373, 406 {D, L, IS}

—Brauer 1868.??.? r#1691: 396 {K}

—McLachlan 1871.09.14 r#353: 233 {BIO, DIS, GD, IS, K, RD: ♂♀, REV, SYN}

—Taschenberg 1879 r#5954: 218 {D, IS}

—Gerstaecker 1894 r#2559: 98 {DIS, MOR}

—van der Weele 1909.01.05 r#420: 43 {DIS, GD, MON, RD: ♂♀, TSP: *Ascalaphus costatus* Burmeister. }

—Navás 1912b.10.31 r#542: 207 {D, IS, K}

—Navás 1913 r#1207: 46 {D, IS, K}

—Banks 1915 r#68: 350 {DIS, SYN, TS, TSP}

—Williner 1945 r#6292: 425, 426 {D, IS, L}

—Orfila 1949 r#5020: 189 {DIS, SYN, TS, TSP}

—Eisner and Adams 1976.04.20 r#2200: 304 {BIO, MOR}

—Henry 1977 r#2877: 190, 192 {BIO, MOR}

—Shetlar 1977 r#5727: 76, 83 {Ph.D. dissertation, nomenclatural acts invalid: DIS, IS, JSYN (part, of *Amoea* Lefèbvre), RD: ♂♀, SYN, TS, TSP}

—Henry 1978a r#2880: 9 {DIS, SYN}

—Penny 1978.09.15 r#5098: 12 {L, IS, SYN}

—Henry 1978b r#2878: fig. 1 {PHY}

—Penny 1982a r#5105: 395, fig. 4 {D, DIS, IS, K, SYN, TSP}

—Penny 1982b r#5103: 619 {BIO, D, DIS, GD, IS, K, MOR, SYN, TSP}

—Oswald and Penny 1991.12.02 r#7138: 28 {SYN, TS, TSP}

—Tjeder 1992 r#7246: 30 {MOR}

—Penny 2002.10.21 r#10230: 178 {D, BIO, GD, IS, K, MOR}

—Ardila and Jones 2012.04.13 r#14570: 40 {D, DIS, GD, IS, MOR}

—Ábrahám 2013.04.30 r#?????: 173 {IS, REV, SYN, TSP}

—Onore et al. 2014.03.30 r#15564: 88, 91 {BIO, MOR}

Ptynx Lefèbvre, 1842

—Lefèbvre 1842.04.?? r#3666: 6 {TSP: given as *Ascalaphus costatus* Burmeister (misidentification); now *Ascalaphus appendiculatus* Fabricius (see "*Type species of Ptynx Lefèbvre, Neuroptynx McClendon and Ascaloptynx Banks*" under "Discussion" below). TS: monotypy. D, K.}

—Rambur 1842.12.31 r#5314: 362 {JSYN (of *Haploglenius* Burmeister)}

—Walker 1853 r#6194: 446 {JSYN (of *Ascalaphus* Fabricius).}

—Hagen 1866 r#460: 458 {JSYN (of *Haploglenius* Burmeister)}

—McLachlan 1871.09.14 r#353: 238 {DIS, GD, IS, K, RD: ♂♀, REV, SYN}

—McClendon 1906.05.?? r#3839: 172 {JSYN (of *Neuroptynx* n. gen., objective replacement name for *Ptynx* Lefèbvre, preoccupied)}

—van der Weele 1909.01.05 r#420: 28, 55 {JSYN (of *Neuroptynx* McClendon)}

—Banks 1915 r#68: 350 {DIS, JSYN (of *Haploglenius* Burmeister), TS, TSP}

—Orfila 1949 r#5020: 189, 190 {DIS, JSYN (of *Neuroptynx* McClendon), TS, TSP}

—Shetlar 1977 r#5727: 96 {Ph.D. dissertation, nomenclatural acts invalid: DIS, MOR, JSYN (of *Neuroptynx* McClendon), SYN, TSP}

—Penny 1978.09.15 r#5098: 12 {JSYN (of *Haploglenius* Burmeister)}

—Penny 1982a r#5105: 398 {JSYN (of *Haploglenius* Burmeister)}

—Oswald and Penny 1991.12.02 r#7138: 28, 51 {DIS, SYN, TS, TSP}

—Penny, Adams and Stange 1997.12.09 r#8867: 42 {SYN}

—Ábrahám 2013.04.30 r#?????: 174 {JSYN (of *Haploglenius* Burmeister)}

Olophthalmus Lefèbvre, 1842

—Lefèbvre 1842.04.?? r#3666: 4, 8 {unavailable (no type material designated), JSYN (of *Haploglenius* Burmeister—see Oswald and Penny 1991)}

Haplogenius [sic] Lefèbvre, 1842

—Lefèbvre 1842.04.?? r#3666: 8 {DIS, ISS}

Neuroptynx McClendon, 1906

—McClendon 1906.05.?? r#3839: 172 {TSP: *Ascalaphus appendiculatus* Fabricius (see "*Type species of Ptynx Lefèbvre, Neuroptynx McClendon and Ascaloptynx*

Banks" under "Discussion" below). TS: monotypy. IS, NN ("*Neuroptynx*" as objective replacement name for *Ptynx* Lefèbvre, 1842, preoccupied by *Ptynx* Moehring, 1758 (Aves) and *Ptynx* Blyth, 1840 (Aves)).}

—van der Weele 1909.01.05 r#420: 55 {D, DIS, GD, RD: ♂♀, SYN, TS, TSP}

—Banks 1915 r#68: 350 {DIS, JSYN (of *Haploglenius* Burmeister)}

—Froeschner 1947 r#2422: 128 {K}

—Orfila 1949 r#5020: 190 {DIS, JSYN (of *Haploglenius* Burmeister), SYN, TS, TSP}

—Shetlar 1977 r#5727: 96 {Ph.D. dissertation, nomenclatural acts invalid: DIS, SYN, TS, TSP}

—Penny 1978.09.15 r#5098: 12 {JSYN (of *Haploglenius* Burmeister)}

—Penny 1982a r#5105: 398 {JSYN (of *Ascaloptynx* Banks)}

—Lago and Testa 1989 r#3608: 12 {SYN}

—Oswald and Penny 1991.12.02 r#7138: 28 {DIS, JSYN (of *Haploglenius* Burmeister), TS, TSP}

Verticillecerus van der Weele, 1909 **new synonym**

—van der Weele 1909.01.05 r#420: 54 {TSP: not designated (*Verticillecerus gerstaeckeri* n. sp). TS: monotypy. D, DIS, GD, MOR, OD: ♀.}

—Navás 1912b.10.31 r#542: 212 {D, IS}

—Navás 1913 r#1207: 52 {D, IS}

—Williner 1945 r#6292: 428 {D, IS}

—Orfila 1949 r#5020: 188 {DIS, SYN}

—Henry 1978a r#2880: 9 {DIS}

—Penny 1978.09.15 r#5098: 14 {IS, L, SYN}

—Penny 1982a r#5105: 401 {D, DIS, GD, IS, K, TS, TSP}

—Nel 1991. ??.?? r#8267: 333 {DIS, MOR}

—Oswald and Penny 1991.12.02 r#7138: 59 {SYN, TS, TSP}

—Ardila and Jones 2012.04.13 r#14570: 44 {DIS, MOR}

—Ábrahám 2013.04.30 r#?????: 184 {D}

Neuroptyngini Navás, 1912 **new synonym**

—Navás 1912b.10.31 r#542: 212 {as tribe}

—Schröder 1920 r#5595: 838 {as tribe}

Neuroptinginos Navás, 1912 **new synonym**

—Navás 1912b.10.31 r#542: 212 {as tribe}

Ascaloptynx Banks, 1915 **new synonym**

—Banks 1915 r#68: 350 {TSP: *Ascalaphus appendiculatus* Fabricius (see "*Type species of Ptynx Lefèbvre, Neuroptynx McClendon and Ascaloptynx Banks*" under "Discussion" below). TS: original designation. DIS, NN ("*Ascaloptynx*" as replacement name for *Neuroptynx* McClendon, 1906, the latter a JSYN of *Haploglenius* Burmeister), SYN}

—Henry 1972 r#2875: 1–22 {BIO, DIS, EVO, IMS, MOR}

—Henry 1976 r#2876: 1–31 {BIO, DIS, EVO, IMS, MOR}

—Henry 1977 r#2877: 179–195 {BIO, DIS, EVO, IMS, MOR}

—Shetlar 1977 r#5727: 96 {Ph.D. dissertation, nomenclatural acts invalid: DIS, JSYN (of *Neuroptynx* McClendon), TS, TSP }

—Henry 1978a r#2880: 9–18 {BIO, DIS, IMS, MOR}

—Henry 1978b r#2878: 75–86 {BIO, EVO, MOR, PHY}

—Penny 1982a r#5105: 398 {D, DIS, GD, IS, K, SYN, TSP}

—Lago and Testa 1989 r#3608: 12 {DIS, JSYN (of Neuroptynx McClendon)}

—Nel 1991. ??.?? r#8267: 332 {BG, DIS, EVO, FOS, GD, MOR}

—Oswald and Penny 1991.12.02 r#7138: 10 {DIS, SYN, TS, TSP}

—Tjeder 1992 r#7246: 34 {BIO}

—Ardila and Jones 2012.04.13 r#14570: 44 {DIS, MOR}

Neohaploglenius Penny, 1982a

—Penny 1982a r#5105: 398, fig. 3 {TSP: *Haploglenius flavicornis* McLachlan. TS: original designation. D, DIS, GD, IS, K, OD: sex not indicated.}

—Penny 1982b r#5103: 626 {D, DIS, GD, IS, K, MOR, TSP}

—Nel 1991. ??.?? r#8267: 333 {DIS, MOR}

—Oswald and Penny 1991.12.02 r#7138: 42 {TS, TSP}

—Tjeder 1992 r#7246: 30 {MOR}

—Penny 2002.10.21 r#10230: 179 {D, IS, GD, K, MOR}

—Ardila and Jones 2012.04.13 r#14570: 44 {DIS, MOR}

—Ábrahám 2013.04.30 r#?????: 173 {DIS, JSYN (of *Haploglenius* Burmeister)}

Etymology and nomenclatural notes.—*Haploglenius*: haploos, haplous (Greek), 'single, simple' + glen– (Greek), 'eyeball, pupil of eye, socket' + –ium (Latin), 'quality or nature of', ='simple-eyed, entire-eyed'. Referring to the entire eyes (as opposed to the divided eyes of ascalaphine owlflies). *Gender*: masculine, from that of the Latin suffix –ius (Oswald, unpublished data).

Diagnosis.—Pleuron with a pair of oblique yellow stripes, each stripe running anteroventrad from wing base to subtending coxa; or, pleuron pattern variable, but without pair of oblique yellow stripes, wing bases narrowed, FW anal angle developed into a process, and antennae with verticils.

Synapomorphies.—antennal flagellum normal, nodes distinctly pale; thorax pruinescence in males and females, present on pleuron only, on oblique stripes; male HW basiposterior margin somewhat convex after anal angle but not distinctly changing angle at Mp_1, and wing not especially narrow; HW pre-cup axillary disk opaque, yellow; presectoral area with 9 to 14 cells; pulvini very small and poorly developed, apex with small apical tuft of intermediately long setae.

Distribution.—Widespread in Western Hemisphere: U.S. to Argentina.

Morphology, biology and ecology.—McLachlan (1871: 226) reported observations of haplogleniines flying in the shade of the Amazon forest and reposing with their wings expanded, and not tectate as in ascalaphine species. Onore et al. (2014) described heliographic signaling in males of a species with a well-developed pronotal valve.

Description.—

Head. Breadth at widest point (of eyes) more or less coequal to that of mesothorax at wing bases when wings folded over back, slightly narrower in some species. Vertex sagittal plates present, often obscure: anterosagittal plate represented as very narrow parasagittal bands divided by epicranial suture, posteriorly divergent; posterosagittal plate narrowly cordate to ovoid, also divided by epicranial suture. Extra-torular sclerites each a narrow band, mesally fused. Paraocular band somewhat narrow, glabrous. Frons often with a diffuse narrow sagittal brown line, this frequently reduced to a dorsomesal spot or absent. Setae at least moderately dense on frons, on vertex dense to rather sparse, in some species wavy. Setosity of mouthparts as in other owlflies (e.g., *Allocormodes*). Eyes entire, often very slightly dorsoventrally oblong, slightly enlarged dorsally in a few species and ventrally in others, often very subtly posteromesally flattened, but dividing sulcus absent. Antennae length variable in spread specimens, from approximately half FW length in some species and species groups to nearly reaching pterostigma in others; flagellomeres usually at least slightly swollen at nodes; internodes glabrous in most species but setose in one species group; verticils absent in most species, but present and distinct in several species groups and closely related species; club shape variable, from pyriform with rounded apices to fusiform and acuminate, surfaces covered in fine setae.

*Thorax. Cervix.*Dorsal cervical plate swollen, weakly to distinctly offset from cervical membrane, bearing long, slender setae. *Pronotum.* Anterior flange narrow, slightly produced dorsad. Medial transverse band narrow overall, very narrow mesally, broadening slightly laterally, posterolaterally produced, sometimes into a long bar-like swelling, usually into a knob, this apically bulbous. Posterior flange produced somewhat dorsoposteriorly, barely covering mesoacrotergite, in males of many species more produced, valve-like, sublaterally articulated, overlapping mesacrotergite and portion of mesoprescutum; ventral surface membranous, membrane contiguous with mesonotal acrotergite, with a dense covering of very fine microsetae, often bearing a thick coating of white crystalline material in males with the valve produced. *Pteronotum*. Base color earthy brown, but often numerous small diffuse yellowish maculations present, in some species groups parasagittal longitudinal stripes present. *Pleuron*. In most species, base color brown and a pale (usually yellow) stripe descending from the posterior portion of each wing base across pleural sclerites to the anterior surface of the subtending coxa, stripes often bearing pruinescence, in two species groups stripes reduced or lost, setae more or less even, usually pale.

Legs. Short, femora and tibiae more or less coequal in length, tarsi slightly subequal. Tibial spurs weakly curved, posterior spur slightly longer than anterior one and extending approximately to apex of third tarsomere on pro- and meso-thoracic legs, second tarsomere on metathoracic leg. Femora and tibia base color yellow, but various faces often darkened with dusky reddish to dark brown pigment; tarsi color variable, from yellow to nearly black, but when darker, terminal tarsomere diffusely reddish distally; tibial spurs and tarsal claws reddish-brown. Coxae with moderately dense, medium length, slender, very pale setae; femora and tibiae with long, stiff, black setae, femora with numerous white setae in one species group.

Wings. Shape variable, generally long and moderately slender with apices posteriorly subacute, in several species groups wings strongly narrowed basally and apices rounded. Venation moderately dense, in a few species costals wide, in a few other species cells subtending R greatly enlarged and irregular. Costal, subcostal and apical areas often fuscous, costals sometimes margined, subcostal area of several species with pseudoveinlets; some species with distinct stripes or patterning. *FW.* Costal area with subcostal veinlets not inclined, except in one species group. Pterostigma variable in shape and color of veins and membrane; density and shape of distal margin of pigment diagnostic for several species groups and species. Presectoral area with ca. six to fifteen cells. Anal area hind margin weakly convex to strongly concave; anal angle expression highly variable, from undeveloped to greatly elongate, shape diagnostic; one to two cell rows distad of Cup + 1a, number or rows and distribution of crossveins diagnostic; second basal cell of marginal row (positioned at base of anal angle) always divided by a crossvein. *HW.* Pre-Mp_1 area margin more or less unexpanded. Anal area with one, two, or three rows of cells, number diagnostic.

Abdomen. In males, slender, length variable, not quite reaching pterostigma when wings folded over the back to extending past wingtips; in females, not reaching to pterostigma, usually much shorter and stouter. *Tergum*. More or less evenly brown, distinct patterns appearing in only a few species; T1 and at least proximal portions of T2 with intermediately dense, intermediately long, wispy, setae, remainder of tergum devoid of long setae. *Sternum*. Coloration variable but subtle, distinct patterns in a few species, mostly devoid of long setae, some intermediately long, wispy setae on S2. *Pleural membrane*. Usually brown and devoid of long setae, several species with irregular pale maculation or three to five oblique yellow stripes, these more often distinct in females.

Male terminalia. Pleuritocavae present at posterior margins of segments 7 and 8 in some species and species groups, variable in size; presence and size diagnostic. Two species groups with distal margins of T8 and T9 “hooded” and T8 and dorsal surface of T9 predominately yellow. Ectoprocts simple. S9 apical margin obtusely angled. Pulvini variable, usually small, often bearing numerous variably long, slender setae. GPC only moderately sclerotized, dorsally notched, at most only partially exerted. Parameres moderately sclerotized, in lateral view usually unproduced, in ventral view simple, shape more or less like cloven hooves of a deer but not curved, proximolateral margins weakly to distinctly differentiated. Pelta moderately sclerotized, more or less narrowly almond-shaped. In one species group GPC sclerotized and greatly exerted, with well-developed, tusk-like parameres, these bounded laterally by very long and exerted pulvini bearing numerous long somewhat robust setae, pelta a sagittal carina.

Female terminalia. Ectoprocts simple. Ventrovalvae elongate, moderately to very narrow. Distivalvae triangular. Linguella unsclerotized, poorly differentiated from surrounding membrane. Interdental space glabrous, interdens small, sclerotized, nipple-like or cone-shaped, absent in one species group.

Discussion.—Much confusion has surrounded the characterization of the genus *Haploglenius*, and it has been subject to numerous interpretations and revisions in its history. Some of this confusion has revolved around the identities of its originally included species and the validity of the generic names that have been proposed to contain them. The synonymical history above designates several new taxonomic and nomenclatural changes, and these are explained in more detail in following sections "*Type species of Ptynx Lefèbvre, Neuroptynx McClendon and Ascaloptynx Banks*" and "*Position of Orphne Lefèbvre*". Some questions have also arisen regarding the monophyly of the genus. These issues are discussed in detail in the cladistic analysis and reviewed below in the section "*Cladistic results and synonymy of Neuroptynx McClendon, Neohaploglenius Penny, and Verticillecerus van der Weele*".

Type species of *Ptynx* Lefèbvre, *Neuroptynx* McClendon and *Ascaloptynx* Banks

Burmeister (1839) proposed the genus name *Haploglenius* for two entire-eyed owlflies he newly described from Brazil, *Ascalaphus costatus* and *Ascalaphus subcostatus*. Lefèbvre (1842) subsequently equated *Haploglenius* to his (invalid) genus *Olophthalmes*, and recognized the priority of Burmeister's name, but did not use it because he didn't know with which species to associate it. In his key to the genera of his tribe “Ascalaphides”, he erected the new genus *Ptynx* with representative species *Ascalaphus costatus* Burmeister, which became the type of *Ptynx* by monotypy. He also erected the new genus *Amoea*, giving as its only named species *Ascalaphus subcostatus* Burmeister; it, too, is type species by monotypy.

Rambur (1842) was the first to recognize *Haploglenius* and the first to observe that Lefèbvre had mis-associated Burmeister’s name *costatus* with the taxonomic species *Ascalaphus appendiculatus* Fabricius. Lefèbvre (1842) had placed *Ptynx* in his entire-eyed group “Olophthalmi” and used as diagnostic characters ‘male with anal claspers visible’ and ‘wings appendiculate’. Of all entire-eyed owlflies in the Americas, this description only matches the previously described north American species *Ascalaphus appendiculatus* Fabricius (or possibly one of its sister species, unknown at the time; see ‘*appendiculatus* species group’, below). The species *appendiculatus* differs from Burmeister’s description of *costatus* in having the costal area only very weakly pigmented or devoid of pigment and the forewing base produced into a long triangular tooth-like appendage. Burmeister characterized *costatus* as having the ‘wing border completely anteriorly fuscous’ and the ‘forewing base subdentate’.

Subsequent revisers (McLachlan 1871, van der Weele 1909, Banks 1915, Orfila 1949, Shetlar 1977) also recognized Lefèbvre’s error and attempted to correct it. However, some of their efforts were not valid under previous versions of the Code (explained in the next paragraph). Rambur (1842), for example, made *Ptynx* a junior synonym of

Haploglenius based on his interpretation that *costatus* is conspecific with *appendiculatus*. McLachlan (1871), in his review of the Ascalaphidae, retained *Ptynx* as a valid genus, but assigned to it characters of *appendiculatus* (and not *costatus*), and designated Lefèbvre's interpretation of *costatus* as a junior synonym of *appendiculatus*. Van der Weele (1909) followed Rambur and McLachlan in treating Lefèbvre's taxonomic concept of *costatus* as a junior synonym of *appendiculatus*, and McLachlan in treating *Ptynx* (preoccupied) as a valid genus, although under the new replacement name *Neuroptynx* proposed by McClendon (1906). Like McLachlan, van der Weele described Lefèbvre's *Ptynx* (as *Neuroptynx*) using characters applicable to *appendiculatus* and not *costatus*. He also designated *costatus* of Burmeister (and not Lefèbvre) as type of *Haploglenius* Burmeister. Banks (1915) interpreted Lefèbvre's *costatus* to be conspecific with that of Burmeister and considered *Ptynx* and its replacement name *Neuroptynx* to be a junior synonyms of *Haploglenius*. He proposed the new name *Ascaloptynx* to bear the taxonomic concept described by van der Weele and designated *Ascalaphus appendiculatus* Latreille [sic] as its type. Orfila observed that *Neuroptynx* and *Ascaloptynx* share a single type species, *Ascalaphus appendiculatus* Fabricius, and thus the two genera are synonyms. Shetlar (1977), in his unpublished dissertation, noted that McClendon (1906) listed only *Ptynx juvenilis* McLachlan under his new replacement name *Neuroptynx* and interpreted this to mean the new genus was monobasic (an incorrect inference—see Art. 67.8); he regarded this as sufficient to eliminate *Neuroptynx* from synonymy with *Ptynx* and *Haploglenius*. He also considered *juvenilis* to be conspecific with *appendiculatus*, and synonymized *Ascaloptynx* under

Neuroptynx, making *appendiculatus* the type species. However, because his work was never published his nomenclatural acts are invalid. Subsequent authors followed slightly different paths in interpreting synonymies. Penny (1978, 1982a) placed *Ptynx* Lefèbvre and *Neuroptynx* McClendon as junior synonyms of *Haploglenius*, and (1982a) *Neuroptynx* "of authors" as junior synonym of *Ascaloptynx* Banks. Henry (1972, 1976, 1977, 1978a, 1978b), in a series of papers dealing with life histories and larval and adult morphology and biology of several owlfly species, treated *Ascaloptynx* as valid, as did Nel (1991). But Lago and Testa (1989) followed Shetlar in regarding *Neuroptynx* McClendon as valid.

As noted in Oswald and Penny (1991), the case of misidentification of the type species of *Ptynx* must be resolved in order to settle its nomenclatorial validity and that of *Neuroptynx*. Whereas the third edition of the Code required revisers to refer such cases to the Commission, the current (fourth) edition allows revisers to select and fix as type either "the nominal species previously cited as type" (Art. 70.3.1), or "the taxonomic species actually involved in the misidentification" (Art. 70.3.2). It seems clear that Lefèbvre (1842) misunderstood Burmeister's *costatus* and based his diagnosis of *Ptynx* on the taxonomic species *Ascalaphus appendiculatus* Fabricius. In accordance with Art. 70.3.2, the taxonomic species *Ascalaphus appendiculatus* Fabricius is here (see synonymy above) selected and fixed as the type of *Ptynx* Lefèbvre, replacing the name *Ascalaphus costatus* Burmeister by virtue of misidentification. *Neuroptynx* McClendon then also takes as type species *Ascalaphus appendiculatus* Fabricius (Art. 67.8), and as the oldest unoccupied name takes priority over *Ptynx*. *Ascaloptynx* Banks, which shares the same type species as *Ptynx* and *Neuroptynx*, becomes junior objective synonym of *Neuroptynx*. All of these names, in turn, are placed as junior subjective synonyms of *Haploglenius*, by virtue of the results of the cladistic analysis presented earlier, which placed *appendiculatus* and closely related species well within *Haploglenius* (see also "*Cladistic results and synonymy of Neuroptynx McClendon, Neohaploglenius Penny, and Verticillecerus van der Weele*", below).

Position of *Orphne* Lefèbvre

Although *Orphne* is an ascalaphine genus, it falls into synonymical history with *Ascalaphus appendiculatus* Fabricius and is treated here.

Lefèbvre (1842) also created the new genus *Orphne* in his key to the "Ascalaphides", and designated as type species *Ascalaphus appendiculatus* Fabricius. He placed it within his split-eyed group "Schizophthalmi" and gave as diagnostic characters 'male pincers not externally visible', 'wings appendiculate' and 'antennae longer than the wings'. The wings of *appendiculatus* are indeed appendiculate, as the name suggests, but the abdomen apex bears elongate processes, the antennae are considerably shorter than the wings, and the eyes are not split but entire. This is another case of misidentification of type species. Rambur (1842) considered Lefèbvre to have had a specimen of his genus *Colobopterus* (=*Ameropterus* Esben-Petersen) in making his diagnosis. Subsequent authors (McLachlan 1871, van der Weele 1909, etc.) also treated Lefèbvre's type designation as an error. Van der Weele (1909) inferred Lefèbvre's taxonomic concept to regard the species *Ascalaphus macrocercus* Burmeister, but as with the problem of *appendiculatus* above, the Code did not formerly allow revisers to fix types in the case of misidentification, and van der Weele's act was not valid. In accordance with Art. 70.3.2, the taxonomic species *Ascalaphus macrocercus* Burmeister is here selected and fixed as the type of *Orphne* Lefèbvre, replacing the name *Ascalaphus appendiculatus* Fabricius by virtue of misidentification.

The objective replacement name *Ascalorphne* was proposed by Esben-Petersen for McLachlan and van der Weele's taxonomic concept of *Orphne*, with *Ascalaphus macrocercus* Burmeister as its type. As the type for both *Orphne* Lefèbvre and Orphne *sensu* McLachlan and van der Weele is now *A. macrocercus* Burmeister, the two genera become objective synonyms and *Orphne* Lefèbvre takes priority. As *Orphne* Lefèbvre and *Orphne sensu* McLachlan and van der Weele are both preoccupied (by *Orphne* Hübner, 1825 (Lepidoptera)), *Ascalorphne* Esben-Petersen is next in line and becomes the valid name for the genus, with its type *A. macrocercus* Burmeister.

Cladistic results and synonymy of *Neuroptynx* McClendon, *Neohaploglenius* Penny, and *Verticillecerus* van der Weele

Penny (1982a), in his review of the New World genera of Ascalaphidae, revised the definition of *Haploglenius* to constitute those entire-eyed species lacking a prominent axillary angle in the FW (= diagnosis of Haplogleniini), having longer antennae than *Ascalobyas*, and expressing one more anal vein in the HW (which he interpreted to be 2A) than *Amoea*. Ardila and Jones (2012) determined that 2A actually strikes the wing hind margin early and explained that what Penny called 2A are in fact aligned crossveins. They suggested redefining the diagnosis of the genus to include those species which have three rows of cells in the anal area of the HW rather than an elongate 2A. They also described the new species *abdominevittatus*, which has three rows in the HW, but also a narrowed FW base with a well-developed axillary angle (anal process), a feature diagnostic for Penny's genus *Neohaploglenius* (which he placed in Verticillecerini). Ardila and Jones placed *abdominevittatus* within *Haploglenius* and suggested additional studies comparing the anatomy of *Haploglenius* and related genera be conducted to determine taxonomic placements.

Taxonomic revisionary work and cladistic analysis performed in this study address these issues. Revisionary results (presented below) dissolve some species-level synonymies and bring to light several new species that collectively, under traditional definitions, would belong within the genera *Neuroptynx*, *Verticillecerus*, and *Neohaploglenius*. The cladistic analysis presented earlier, however, demonstrates that these genera represent highly derived clusters at the ends of pectinate lineages within a large monophyletic clade (A3 Fig. 1 nodes 17, 23, 25, 33). Maintaining them as valid renders the larger clade paraphyletic, unless each branch is also given a new name, an unwieldy task that would merely serve to bloat the literature with many unnecessary new names for monobasic entities. In order to maintain stability (via simplicity) and observe overall monophyly, the names of these small genera are sunk (see synonymy above). The large containing clade (A3 Fig. 1 node 17) is redefined here as an enlarged *Haploglenius*, and the nested genera (A3 Fig. nodes 23, 25, 33) are made junior subjective synonyms thereof. Nevertheless, as it is useful to preserve utility in diagnosis and identification, new species groups are here created to contain the species that constitute these former genera and to retain the diagnostic features of those former genera, where still applicable; a few more species groups (A3 Fig. 1 nodes 30, 34) are additionally erected to contain other demonstrably unified species also expressing clear diagnostic traits. See "Discussion" section under species group headings for more details.

Included species.—*acuminatus* n. sp.; *abdominevittatus* Ardila and Jones; *angulatus* Gerstaecker; *appendiculatus* (Fabricius); *aquilonius* n. sp.; *brunneus* n. sp.; *costatus* (Burmeister); *cuboides* n. sp.; *decoratus* n. sp.; *decorus* Ábrahám; *elongatus* n. sp.; *extensus* Banks; *flavicornis* McLachlan; *gerstaeckeri* (van der Weele); *handlirschi* van der Weele; *juvenilis* (McLachlan) ; *legnotos* n. sp.; *luteus* (Walker); *neoguineensis* Navás; *normani* n. sp.; *peruvianus* van der Weele; *procerus* n. sp; *reticulatus* Navás.

***Key to the extant species of* Haploglenius**

(adult males and females; except:

males only: *acuminatus* n. sp., *aquilonius* n. sp., *elongatus* n. sp.;

females only: *legnotos* n. sp.)

1. FW: considerably narrowed at base; anal angle developed into a process, this acute and triangular to elongate and produced, and wing hind margin distad of process distinctly concave 2

1’. FW: broad to at most only slightly narrowed at base, anal angle at most only weakly produced, obtuse; hind margin distad of angle slightly concave to convex 9

2(1). HW anal area with three rows running parallel to CuA; pleuron variegated, lacking parallel oblique pale stripes [Colombia, Venezuela] (*reticulatus* species group, part) .... ***abdominevittatus* Ardila and Jones**

2’. HW anal area with one or two cell rows; pleuron with oblique stripes present or absent 3

3(2’). Antennae lacking verticils (*flavicornis* species group) 4

3’. Antennae with verticils 5

4(3). HW somewhat narrowed at base: height of HW anal cells in both rows subtending CuP conspicuously greater than cells in medial triangle [Brazil, Costa Rica, El

Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Venezuela] .... ***angulatus* (Gerstaecker)**

4'. HW strongly narrowed at base: anal cells in both rows subtending CuP very small, coequal in height with cells in medial triangle, and similar in height, width, and shape to each other [Guatemala, Costa Rice, Panama] ..... ***flavicornis* (McLachlan)**

5(3'). Antennae in distal two thirds with numerous internodal setae; pleuron pattern variegated, lacking parallel oblique pale stripes (*appendiculatus* species group) ... 6

5'. Antennae in distal two thirds with internodes glabrous; pleuron with oblique parallel pale stripes (*gerstaeckeri* species group) 8

6(5). Distal cells of costal area not divided by oblique crossveins; wings devoid of pigment; males: pronotum with an articulable valve; abdomen very slender, extending beyond apices of wings in unspread specimens [Honduras; Mexico: Yucatan] .... ***elongatus* n. sp.**

6'. Distal cells of costal area divided by oblique crossveins; subcostal area tinged with brown color; males: pronotum without an articulable valve; abdomen only moderately slender, not extending past apices of wings in unspread specimens 7

7(6'). Abdominal tergites 3-7 with diffuse to well-defined often triangular black maculae, these positioned both anterior and posterior to tergal lateral antecostal scars; S3 black longitudinal stripes with well-defined edges along entire length;

males: distal margin of T3 bearing an erect elongate process, this highly variable in size and shape, but often slender with a forked apex [northwestern Mexico; U.S.: central Texas and Oklahoma westward] .... ***juvenilis* (McLachlan)**

7’. Abdominal tergites 3-7 lacking maculations near antecostal scars, or if present, only a very diffuse spot around slit; S3 longitudinal black stripes posteriorly with diffuse margins, often fading before striking posterior transverse black stripe; males: T3 distal margin without a process, although sometimes a very small nub may be present [Eastern U.S.: eastward from eastern Texas and Oklahoma] .... *a****ppendiculatus* (Fabricius)**

8(5’). Axillary angle of forewing short, triangular, wider at base than long; antennae slightly longer than half of forewing length in spread specimens; presectoral cells undivided [Brazil, Bolivia, Paraguay] .... ***gerstaeckeri* Van der Weele**

8’. Axillary angle of forewing long and acuminate, approximately three times longer than width at base, curving slightly distad of wing base; antennae approximately three-fourths forewing length in spread specimens; distal presectoral cells divided by oblique crossveins [south central Brazil] .... ***acuminatus* n. sp.**

9. Pterostigma yellow and distal margin of pigment strongly crescent shaped, extending along FW margin, breadth of pterostigma >3x height (*extensus* species group) ... 10

9'. Pterostigma pigment color variable, distal margin shape variable, but usually straight or only slightly crescent-shaped, with pigment not extending along FW margin 13

10(9). Cells subtending R greatly broadened, width of at least several mesal-most cells >3x height, often (in males) with a distinctive pattern of broad anterolateral margining 11

10'. Cells not broadened, width approximately equal to height; anterolateral margining narrow to absent, without a distinctive reticulate pattern 12

11(10). Pteronotum with very thin and rather weakly expressed parasagittal stripes; large cells subtending R somewhat irregular, and without, or with very few, smaller intercalary cells; expression of margining pattern variable, from very reduced (often in females) to heavily margined (often in males) [Brazil, Ecuador, Peru] .... ***decoratus* n. sp.**

11'. Pteronotum without parasagittal stripes; large cells subtending R highly irregular, with small intercalary cells separating them, and lateral margins of cells heavily margined, giving cell row a reticulate or net-like appearance [French Guiana] .... ***decorus* Ábrahám**

12(10’). HW with two rows of anal cells, some cells in posterior row often divided by crossveins; cell row subtending R infuscate, forming a stripe [Bolivia] .... ***extensus* Banks**

12’. HW with three rows of anal cells; cells subending R not infuscate, but very narrowly anterolaterally margined, accentuating cells’ cube-like shape [Brazil: Rondônia] .... ***cuboides* n. sp.**

13(9’). FW anal area cell row divided by oblique crossveins 14

13’. FW anal area cell row not divided by oblique crossveins 21

14(13’). Pterostigma veins dark brown, membrane pigment brown, often extending past pterostigma along margin into apical area [Brazil, Honduras] .... ***handlirschi* van der Weele**

14’. Pterostigma veins and membrane pigment pale to yellow, occasionally margined with dark brown pigment 15

15(14’). FW hind margin distad of axillary angle convex 16

15’. FW hind margin distad of axillary angle concave 17

16(15). Distal domain of medial triangle >2.5xwidth at base, comprising two to four often narrowed cells [Costa Rica, Honduras, Panama] .... ***procerus* n. sp.**

16’. Distal domain of medial triangle <2xwidth at base,comprising two to three not especially narrowed cells [Bolivia, Brazil, Ecuador, Peru] .... ***peruvianus* van der Weele**

17(15’). Antennae moderately long, reaching about two thirds distance from wing base to pterostigma, not robust, nodes not swollen, color variable 18

17’. Antennae long, reaching nearly to pterostigma in spread specimens, robust, swollen and darkened at nodes, diffusely paler at internodes near antennomere base; males: pronotal valve poorly developed, not articulable; acrotergite not bilobed (*reticulatus* species group, part) 20

18(17). Antennae basal flagellomeres with verticils; males: pronotal valve somewhat well-developed, articulable; acrotergite simple, not bilobed [Argentina, Bolivia, Brazil, Colombia, Panama] .... ***costatus* (Burmeister)**

18’. Antennae without verticils; males: pronotal valve well-developed, articulable; acrotergite bilobed 19

19(18). Labrum yellow [Bolivia, Brazil, French Guiana, Guyana, Peru, Suriname] .... ***luteus* (Walker)**

19’. Labrum dark brown, at least in distal half [Bolivia, Brazil, Colombia, Ecuador, Mexico, Panama, Peru] .... ***brunneus* n. sp.**

20. Costal cells width more or less coequal to height [Venezuela] .... ***aquilonius* n. sp.**

20. Costal cells more than twice as wide as high [Ecuador, Peru] .... ***reticulatus* Navás**

21(13'). HW anal area with two cell rows 22

21'. HW anal area with three cell rows 23

22(21). Cell row subtending R in both wings infuscated with dark brown pigment, this extending past pterostigma to fill most of apical area; pterostigma veins dark brown, pigment yellow [French Guiana] .... ***legnotos* n. sp.**

22'. Cell row subtending R not infuscated, apical area without pigment; pterostigma veins dark brown and pigment pale brown [Argentina, Bolivia, Brazil, Peru] .... ***normani* n. sp.**

23(21'). Antennae with several verticils near base; frons yellow to dull brownish, more or less concolorous with clypeus; males: acrotergite not bilobed; pleuritocavae absent [Argentina, Bolivia, Brazil, Colombia, Panama] .... ***costatus* (Burmeister)**

23'. Antennae without verticils; frons distinctly darker than clypeus, reddish or smoky amber brown; males: acrotergite bilobed; pleuritocavae long and curving 24

24(23'). Mesal cells of costal area, at least in HW, wider than their height; subcostal veinlets usually diffusely but darkly margined; labrum dark brown, at least in distal half [Colombia, Costa Rica, Ecuador] .... ***neoguineensis* Navás**

24’. Mesal costal area cells approximately equal to or narrower than their height; subcostal veinlets margined or not; labrum yellow or dark brown 25

25(24’). Labrum yellow [Brazil, Bolivia, French Guiana, Guyana, Peru, Suriname] .... ***luteus* (Walker)**

25’. Labrum dark brown, at least in distal half [Bolivia, Brazil, Colombia, Ecuador, Mexico, Panama, Peru] .... ***brunneus* n. sp.**

gerstaeckeri *species group*

Diagnosis.—Somewhat small species, FW lengths 29-36 mm. *Head*. Vertex slightly swollen but not bilobed. Antennae basal 6–12 flagellomeres subapically with long slender black verticils. *Thorax*. In males, pronotal valve developed or not. Pleuron with paired oblique pale stripes. *Legs*. Tarsi pale brown to yellow, concolorous with pale surfaces of tibia. *Wings*. Narrowed at bases, apices evenly rounded. Costal area with subcostal veinlets distinctly inclined toward apex of wing. Regions near or along leading edges of wings with reddish brown maculation running length of wing. Pterostigma with distal margin of pigment long and straight. FW anal area hind margin distinctly concave, anal angle well developed, short and triangular to elongate, acuminate and slightly curved, a single very narrow cell row distad of Cup + 1a; HW pre-Cup axillary disk yellowish, medial triangle distal domain absent, anal area with one or two complete row of cells. *Abdomen*. Evenly dull reddish brown, without distinct patterning. *Males*. GPC not everted. Parameres unproduced. *Females*. Interdens present.

Synapomorphies.—labrum reddish amber; pteronotum longitudinal stripes present, sublateral, dark; tarsi evenly yellow.

Discussion.—This group represents the former genus *Verticillecerus* Van der Weele and includes one new species. Van der Weele (1909) suggested that *Verticillecerus* must be closely related to *Neuroptynx* on account of "the long Postcosta [HW Cua] and the short Ramus obliquus [HW Mp_{2p}], short thick antennae and long hind spurs". *Haploglenius gerstaeckeri* also strongly resembles *Haploglenius costatus* and *Haploglenius normani* in gross appearance (but see discussion under those species for differentiating features). This species group appears to be a rather widespread but very uncommonly collected.

Williner (1944) designated a male from Argentina as an allotype for the genus *Verticillecerus*. This specimen is not from a type series that includes van der Weele's holotype (only a single specimen was described, thus no such type series exists).

Haploglenius gerstaeckeri *(van der Weele, 1909) new combination*

(A3 Figs. 35–36, 85)

Verticillecerus gerstaeckeri van der Weele, 1909

—van der Weele 1909.01.05 r#420: 54, fig. 27 {OD: ♀, D, ET. TS: not indicated [holotype by monotypy]. TL: Paraguay. TR: EMAU. Type specimen not examined (see "Discussion" below).}

—Navás 1912b.10.31 r#542: 212 {D, GD}

—Navás 1913 r#1207: 52 {D, GD}

—Penny 1978.09.15 r#5098: 14 {L, GD}

—Penny 1982a r#5105: 401 {D, DIS, GD, TSP (of *Verticillecerus* van der Weele, 1909)}

—Oswald and Penny 1991.12.02 r#7138: 59 {TSP (of *Verticillecerus* van der Weele, 1909)}

—Ábrahám 2013.04.30 r#?????: 184 {GD, SYN, SR}

Verticellecerus [sic] *gerstaeckeri* van der Weele, 1909

—van der Weele 1909.01.05 r#420: 55, fig. 27 caption {ISS}

Werticillecerus [sic] *gerstaeckeri* van der Weele, 1909

—Williner 1945 r#6292: 428, fig. 3 {D, DIS, GD, ISS, MOR, SR, TL, TR, TS}

—Oswald and Penny 1991.12.02 r#7138: 59 {SYN}

Haploglenius bolivianus Navás, 1927 **new synonym**

—Navás 1927 r#823: 1 {OD: ♂, DIS. TS: holotype by monotypy. TL: Buenavista, Departamento de Santa Cruz, Bolivia. TR: NAVC (see Ábrahám 2013). Type specimen not examined (see "Discussion" below).}

—Navás 1929.02.?? r#860: 109 {D, GD}

—Penny 1978.09.15 r#5098: 12 {GD, L}

—Penny 1982a r#5105: 398 {D, MOR}

—Penny 1982b r#5103: 620 {DIS, JSYN (of *Ascalaphus luteus* Walker), MOR, TL, TR, TS}

—Montserrat 1986 r#4301: ? {TR}

—Ábrahám 2013.04.30 r#?????: 184 {GD, DIS, MOR, TR, TS}

Neohaploglenius rondonianus Penny, 1982

—Penny 1982b r#5103: 626, fig. 10, map 8 {OD: ♂♀, D, GD, ET, HAB. TS: holotype ♂ by original designation. TL: "Brasil: Rondônia Vilhena". TR: INPA. Type specimen not examined (see "Discussion" below).

—Penny 2002.10.21 r#10230: 179 {GD}

—Ábrahám 2013.04.30 r#?????: 184 {JSYN (of *Verticillecerus gerstaeckeri* van der Weele), TL, TR, TS}

<u>Etymology and nomenclatural notes</u>.—*gerstaeckeri*: a Latinized noun in the genitive case. Named for C. E. A. Gerstaecker (1828-1895), a prominent German zoologist

and entomologist in whose collection at the Greifswald Museum van der Weele (1909) discovered the new species, among specimens of *H. costatus*.

Diagnosis.—Head slightly smaller than in other species. Antennae rather short, not reaching past second fork of Rs in spread specimens. Verticils on basal antennomeres numerous. Pteronotum with lateral longitudinal diffuse dark stripes. Subcostal veinlets oblique in distal half of costal area. Presectoral and radial area cells subtending R not secondarily divided. FW anal process developed, short, triangular. HW pre-Cup axillary disk translucent yellowish.

Autapomorphies.—male HW basiposterior margin slightly produced at angle, then concave until distad of Mp_{2p}; HW anal area with two cell rows roughly parallel to Cua.

Distribution.—Bolivia, Brazil, Paraguay.

Description.—

Size (mm). Male: length of body 28–32, abdomen 20–24, forewing 29–30, hind wing 26–27, antennae 16–18. Female: length of body 24–28, abdomen 17–21, forewing 31–36, hind wing 28–33, antennae 18–19.

Head. Width at eyes approximately coequal to width of mesothorax at wing base. Occiput base color reddish brown, pattern consisting of irregular diffuse yellow blotches positioned laterally. Vertex slightly swollen, not bilobed, sandy to reddish brown; setae moderately dense, mixed dark brown and very pale yellow or grayish white, moderately long, slender. Extra-torular sclerites concolorous with frons. Paraocular band dull dark brown near antennae, otherwise dusky dark brown. Frons dusky orange; setae moderately dense, mixed dark brown and golden. Clypeus yellow to orangish red, sometimes slightly darkened laterally. Labrum amber yellow. Mandibles concolorous with mesal part of clypeus basally, dark reddish brown in apical half. Labium pale amber orangish, with a thin dark brown sagittal line. Eyes very slightly dorsoventrally oblong, in anterior view symmetrical, in lateral view very slightly larger in ventral half. Antennae somewhat short, not reaching past second fork of Rs in spread specimens, flagellomeres slightly swollen at nodes, flagellum pale yellow to amber red, basal 6-8 flagellomeres preapically with four to seven long slender anteriorly-directed black verticils, these absent on dorsolateral surfaces; clubs narrow elongate pyriform with apices acuminate, pale yellow, anterior face slightly dusky, all surfaces covered in fine dark setae.

Thorax. Cervix. Dorsal cervical plate setae pale yellow. Cervical sclerite dull dark yellowish or reddish brown. Anterior flange a narrow collar, weakly produced dorsad. Medial transverse band posterolaterally produced into a long bar, apically somewhat bulbous. Posterior flange of females covering mesoacrotergite, in males valve-like, overlapping acrotergite nearly to midpoint of anterior swelling of mesoprescutum, ventral surface often with coating of white crystalline material. Pronotum base color medium to sandy reddish brown, all nota laterally dusky dark reddish brown and velvety, valve dorsal surface in males reddish brown. All surfaces bearing medium to somewhat long, slender, dark brown setae with some pale white setae mixed in dorsomesally. *Pteronotum*. Medium sandy brown dorsally, dark reddish brown sublaterally to wing bases, giving appearance of dark lateral longitudinal superalar stripes, lateral surface of mesoprescutum diffusely yellow; velvety spots of metascutum dark brown; entire surface of pteronotum covered with moderately dense, moderately long, fine, dark brown setae. *Pleuron* base color brown, a pair of oblique yellow stripes descending from wing bases to venter; pleural setae moderately dense, moderately long, fine, predominately pale yellow with some dark brown setae mixed in near wing bases, stripes sometimes with a light dusting of pruinescence.

Legs. Femora and tibiae pale yellow, anterolateral surfaces of first two legs often dark amber red, femora sometimes completely. Tarsi pale, concolorous with pale surfaces of tibia. Coxae setae very pale yellow or white; antennal comb setae golden, becoming black along anterolateral margin.

Wings. Dimension and shape. Moderately long, relatively broader than in congeners, narrowed at bases, apices evenly rounded. *Venation/cells.* FW. Costal area with subcostal veinlets distinctly inclined toward apex of wing, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with five to six forked and unforked veinlets, proximal veinlets dark reddish brown, distal veinlets yellow; membrane mesally cream to reddish, somewhat translucent to opaque, distal margin of pigment long and straight. Deltus brown, often darkening and becoming opaque anteromesally. Presectoral area with ca. eleven to fourteen cells. Rs with five to six forks. $Mp_2 + Cua_1$ evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. eleven to thirteen irregular but more or less complete rows of cells. Cubital triangle distal domain with one to three cells. Anal area hind margin distinctly concave, anal angle developed into a triangular tooth-like process, a single narrow cell row distad of Cup + 1a, cells undivided by crossveins. *Color and patterning.* Most veins and veinlets pale to dark reddish brown; Sc and R becoming yellow in apical two-fifths of wing, continuing into posterior veinlets of pterostigma. Wing membranes sometimes tinged with brown pigment. Costal and subcostal areas fuscous, veinlets often margined and darker, pigment very narrowly absent along anterior margin of basal costal cells. Presectoral and proximal half of radial area with anterior portions of cells subtending R tinged brown. HW. As in forewing except as follows. Mp_2 fork angle approximately 90°. Medial triangle distal domain reduced to a single cell. Pre-Cup axillary disk translucent yellowish. Pre-Mp_1 area margin concave. Anal area with two narrow rows of cells, dividing crossveins absent in distal cells near Mp_{2p}.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly dull reddish brown; T1 and T2 with moderately dense, moderately long, wispy setae, these pale yellow mesally and brown laterally, remainder of tergum devoid of long setae. *Sternum*. Mostly evenly pale reddish brown, S1 to S3 sometimes diffusely yellow, with a narrow dark brown sagittal line; mostly devoid of long setae, some moderately long, wispy, brown and golden brown setae on S1 and S2. *Pleural membrane*. Dark brown, often with irregular yellow maculations, devoid of long setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible, ectoprocts and S9 pale reddish brown. *Macerated specimens.* S9 apical margin obtusely angled. Pulvini extremely reduced, essentially indistinguishable from gonosaccal membrane, only evidenced by short, slender, very pale setae. GPC short, somewhat sclerotized; in lateral view dorsal margin weakly arched in basal half, subapically very weakly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view moderately broad laterally. Parameres in ventral view with proximolateral margins weakly differentiated. Pelta sclerotized, narrowly almond shaped, apices weakly blunt or truncated.

Female terminalia. Unmacerated specimens. Ventrovalvae dull reddish brown, distivalvae and ectoprocts pale yellowish brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. two and a half times width. Linguella weakly differentiated from surrounding membrane, bearing several short, stiff, very slender setae. Interdental space round. Interdens sclerotized, short, pin-like.

Variation. One female from Bahia, Brazil (JRJ_01042) appears to be melanistic, having dark brown wings and slightly more intense coloration.

Type material examined.—Not available for this study.

Additional material examined.—*Bolivia*: Beni (USNM: 1 ♂, JRJ_01040 [A3 Fig. 35]). *Brazil*: Bahia (INPA: 1 ♀, JRJ_01042); Goiás (UNESP: 1 ♂, JRJ_01043); Minas Gerais

(UMSP: 1 ♂, JRJ_01039.); Rondônia (FSCA: 1 ♀, JRJ_01044). *Paraguay*: Central (MFNB: 1 ♀, JRJ_01041 [A3 Fig. 36]).

Morphology, biology and ecology.—Label data for one specimen indicates it was collected at light. Elevations recorded on collection labels range from 200 to approximately 750 m.

Discussion.—Although the holotype was not examined, van der Weele's (1909) description and photograph provided enough detail to confidently identify specimens in loan material.

This species is somewhat diminutive and bears a resemblance to smaller individuals of other *Haploglenius* species, including *costatus* and *normani*. It can be distinguished by numerous features, including its smaller overall size, the head relatively smaller compared to the thorax, shorter yellow antennae with more numerous and elongate verticils, the shorter pronotal valve on the pronotum of males, yellow tarsi, oblique subcostal veinlets, denser wing venation, etc. In *normani* the pronotal valve is developed but even smaller, the wing bases are not as narrow, the anal angle is less produced, and the pterostigmata are darker and more distinctive.

Ábrahám (2013) examined the type specimen of *rondonianus* and determined it to be conspecific with *gerstaeckeri*. The type displays the diagnostic features of *gerstaeckeri* , but as Ábrahám points out, portions of Penny's description seem to conflict with the specimen and with the concept of *gerstaeckeri* (see 'Discussion' for *normani* below).

Penny (1982b), relying on a brief diagnosis provided by Navás (1929) for *Haploglenius* species, argued that *Haploglenius bolivianus* Navás, 1927 is probably conspecific with *luteus*, on the basis that only *luteus* also has clear costal margins. However, based on observations made in this study, *luteus* often has the costal region infuscate, and other species also have clear costal margins (*reticulatus*, *abdominevittatus*), including teneral specimens of most species. A careful reading of Navás's original description, however, reveals that he only stated the base of the HW costal area to be pigmentless. His description goes on to provide several additional clues that all seem to demonstrate he instead had before him a specimen of *gerstaeckeri*. He stated that the face and antennal clubs were yellow, the pterostigma pale, the costal and subcostal areas light rusty red, the HW costal area base colorless, and the HW pterostigma slightly tinged with rusty color. He also stated that the specimen resembled *costatus* in the form of the axillary angle of the FW, but said the specimen was smaller in stature. He also mentioned it appeared teneral, a feature of gerstaeckeri, in which the wing membranes are rather thin and dull glossy. Considering other species occurring near the type locality of *bolivianus*, a match cannot be made to *normani*, which has dark pterostigma veins, nor to *brunneus*, which has a distinctly brown labrum, nor to *peruvianus*, which has the anal margin of the FW convex, all features which differ from Navás's original description. The distribution of *luteus* does not closely approach that of *bolivianus*. A few female specimens with morphotypes similar to *costatus* were found in loan material (see ‘Variation’ and ‘Discussion’ for *costatus*), but they have dark-veined pterostigmata and the costal areas are not rusty red. Specimens of *gerstaeckeri*, however, have been collected north, south and west of Buena Vista, Bolivia. The best confirmation of this hypothesis would be to examine Navás’s type specimen; unfortunately, it was kept in Navás’s personal collection and was probably destroyed during the Spanish Civil War (see Ábrahám 2013).

Haploglenius acuminatus *new species*

(A3 Fig. 37, 85)

Etymology and nomenclatural notes.—*acuminatus*: acuminatus (Latin), ‘pointed, sharpened’. Named for the elongate and sharp-tipped anal process of the forewing.

Diagnosis.—Verticils on basal antennomeres numerous. Pteronotum lateral longitudinal stripes weak or absent. Subcostal veinlets oblique in distal third of costal area. Presectoral and radial area cells subtending R secondarily divided. FW anal process developed, elongate, strongly acuminate, apex curving distad. Pre-Cup axillary disk dark reddish brown. Female: Unknown.

Autapomorphies.—FW anal angle very well developed and produced, lateral margins of process mesally parallel and slightly curving, apex strongly acuminate; HW pre-cup axillary disk opaque, brownish red; FW with secondary division of cells subtending r distad of Rs origin and proximad of first Rs fork, many more than four cells irregularly divided; basal cell of HW costal area opaque over entire surface, dark reddish brown; HW mesally darkened; cells subtending R in radial area thickly margined; FW pterostigma with first veinlet associated with pigment commencing considerably proximal to Sc-R anastomosis; pterostigma pigment only loosely associated with aggregated veins, partially overlapping them proximally and distally; FW pterostigma pigment distal margin shape diffuse, irregular.

Distribution.—Brazil: Goiás.

Description.—

Size (mm). Male: length of body 35, abdomen 27, forewing 30, hind wing 27, antennae 22.

Head. Width at eyes approximately coequal to width of mesothorax at wing base. Occiput reddish brown near cervical membrane, yellow laterally. Vertex slightly swollen, not bilobed, dark sandy reddish brown; setae moderately dense, dark brown with some pale yellow mixed in, moderately long, slender. Extra-torular sclerites pale reddish brown. Paraocular band dull dark brown, paler near orbital sclerite, yellowish near margin of frons and clypeus. Frons dusky dark orange; setae moderately dense, golden, laterally dark brown. Clypeus, labrum and mandible bases dull reddish brown, mandibles dark reddish brown in apical half. Labium pale amber red, with a thin dark brown sagittal line. Eyes very slightly dorsoventrally oblong, very slightly larger in ventral half, posteromesally slightly flattened. Antennae flagellomeres very slightly swollen at nodes, flagellum pale yellowish red in basal half, becoming dark reddish brown in distal half, ca. basal 12 flagellomeres with subapical whorls of long slender black verticils; clubs elongate, asymmetrically fusiform, with apices subacuminate, dull pale brown, all surfaces covered in fine dark setae.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite dull dark reddish brown. Anterior flange very narrow, weakly produced dorsad. Medial transverse band posterolaterally produced into a long bar, apically somewhat bulbous. Posterior flange barely covering mesoacrotergite, not valve-like, white coating absent. Pronotum base color brown, anterior flange and medial transverse band sublaterally diffusely yellow, posterior flange sublaterally with anterior and posterior surfaces narrowly yellow. All surfaces bearing somewhat long, slender, dark brown setae. *Pteronotum*. Brown, lateral surface of mesoprescutum diffusely yellow; velvety spots of metascutum dark reddish brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, dark brown setae. *Pleuron* dark reddish brown, a pair of narrow oblique yellow stripes descending from wing bases to venter; pleural setae moderately dense, moderately long, fine, predominately pale yellow with some dark brown setae mixed in near wing bases, stripes with pruinescence.

Legs. Pro- and mesothoracic femora reddish brown, metathoracic femora pale yellow, with posterolateral surfaces reddish brown, tibiae pale yellow with anterolateral surfaces reddish brown. Tarsi pale yellow, concolorous with pale surfaces of tibia.

Coxae setae pale yellow on prothoracic legs, white on meso- and metathoracic legs; antennal comb setae golden.

Wings. Dimension and shape. Only moderately long, somewhat broad relative to other haplogleniinaes, strongly narrowed at bases, apices evenly rounded. *Venation/cells.* FW. Costal area with subcostal veinlets distinctly inclined toward apex of wing in apical fourth, cell width and height more or less coequal in proximal half, width narrowing in apical fourth. Pterostigma poorly defined, with ca. six forked and unforked dark reddish brown veinlets; membrane densely imbedded with dark reddish brown granules, slightly opaque, proximal margin of pigment indistinct, distal margin long and straight. Deltus dark reddish brown, somewhat opaque. Presectoral area with twelve cells, distal four to five cells divided by irregular crossveins. Cells subtending R in proximal two-thirds of radial area also divided by irregular crossveins. Rs with seven to eight forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine rather well-formed rows of cells. Cubital triangle distal domain short, with two cells. Anal area hind margin distinctly concave, anal angle developed into an elongate curving process, about four times longer than width at base, a single very narrow cell row distad of Cup + 1a, cells undivided by crossveins. *Color and patterning.* C pale yellow, other veins and veinlets medium to dark reddish brown; Wing membranes sometimes tinged with brown pigment. Costal area with subcostal veinlets margined in proximal two thirds, costal cells becoming nearly completely fuscous in distal fourth of area. Subcostal area completely fuscous. Presectoral and cells in radial area subtending R, basal portions of mediocubital area and cubital triangle fuscous, reddish brown. HW. As in forewing except as follows. Mp_2 fork angle less than 90°. Medial triangle distal domain essentially absent. Pre-Cup axillary disk dark reddish brown. Pre-Mp_1 area margin distinctly concave. Anal area in proximal third with two narrow rows of cells, posterior row then obliterated, anterior row narrow and continuingto Mp_{2p}.

Abdomen. Not quite reaching to pterostigma with wings folded back. *Tergum*. Evenly dull reddish brown; T1 and T2 with moderately dense, moderately long, wispy setae, these dark brown with some pale yellow mixed in, remainder of tergum devoid of long setae. *Sternum*. Evenly pale reddish brown; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Reddish brown.

Male terminalia. Unmacerated specimens. Ventrovalvae dull reddish brown, distivalvae and ectoprocts pale yellowish brown. Ectoprocts produced distodorsad very slightly. *Macerated specimens.* Not available.

Variation. Unknown.

Type material examined.—*Holotype* (A1 Fig. 37), **new designation**, male, Brazil, in INPA collection: “BRASIL, GO, Caldas Novas, Parque Est. Serra de Caldas Novas, 1.000 m /// 17°46'13"S - 48°39'22"W 22-23.iii.2008, Luz J.A. Rafael & F.F. Xavier F°. /// HOLOTYPE Haploglenius acuminatus Jones ♂ design. J. R. Jones 2014 /// JRJ_01045”. Condition: excellent; antennae and wings spread, right middle leg missing, wing posterior margins with a few dings.

Additional material examined.—None available.

Morphology, biology and ecology.—The holotype was collected at light at approximately 740 m (based on label GPS coordinates; the label elevation was stated as 1000 m).

Discussion.—This is a very charismatic small species, with the longitudinal stripes in the wings rather reddish. The holotype was collected approximately 50 kilometers from the collection site of a specimen of *gerstaeckeri*, indicating that these sister species are likely sympatric through at least some part of their range.

appendiculatus *species group*

Diagnosis.—*Head*. Breadth at widest point (of eyes) very slightly narrower than that of mesothorax at wing bases when wings folded back. Vertex setae long, slender and slightly wavy, mixed black and pale gray. Frons setae white. Antennae somewhat short, not reaching past third fork (and usually second) of Rs in spread specimens; internodes setose on distal two thirds; basal 6–10 flagellomeres with distal margin (node) bearing black verticils exceeding length of previous flagellomeres. *Thorax*. Pronotum setae slender and black with wispy pale yellow or white setae mixed in; in males, pronotal valve developed or not. Pteronotum with or without pale parasagittal longitudinal stripes. Pleuron evenly yellow to variegated, often pruinescent, paired oblique pale stripes absent. *Legs*. Femora with numerous white setae. *Wings*. Wings strongly narrowed at base, more so in HW, apices evenly rounded; pterostigma small, pigment weakly expressed, distal margins diffuse; FW deltus devoid of pigment; FW anal area hind margin distinctly concave, anal angle well developed, elongate triangular and tooth-like, a single very narrow cell row distad of Cup + 1a; HW pre-Cup axillary disk very pale, translucent; anal area with one complete row of cells. Cell membranes setose in apical half of wings. *Abdomen*. Dorsum with or without dark maculae ornamenting antecostal scars. Venter often with distinct patterns of alternating dark and pale longitudinal and transverse stripes. T1 to T3 with moderately dense, long, somewhat slender, mixed black and white setae, these transitioning to somewhat short, slender, stiff black setae along entire tergum. *Males*. Nearly as long as to slightly longer than wings when folded over back, slender, cylindrical; T2 acrotergite somewhat elongate, coequal in length to T2; in lateral view T2 and proximal half of T3 dorsally at least slightly arched or humped. GPC everted; parameres sclerotized, reddish-brown, produced as dorsolaterally curving tusks partially hidden laterally by pulvini, joined mesally by pelta, the latter expressed as a sagittal carina; pulvini long, apically bulbous, with numerous long, stiff, slender, black setae, ectoprocts simple. *Females*. Ventrovalvae in lateral and ventral views very elongate and narrow. Interdens absent.

Synapomorphies.—antennae with verticils on nodes nearly to club, those on basal nodes longer than three flagellomeres, much shorter on successive nodes; antennal internodal setae present, numerous; antennal club pyriform, apex blunt; pronotum and mesoprescutum setae of males somewhat sparse, long, stiff, mostly brown with some medium length wispy gray mixed in; pleuron variegated, predominantly yellowish, with a short, broad, diffuse, pale, mesal longitudinal stripe; subalar setae dense, long and white, concentrated into a tuft on mesanepimeron; thorax pruinescence often present, covering entire pleuron and notum; deltus completely devoid of pigment or pigment very faint; cells subtending R in presectoral area without pigment; FW pterostigma with first veinlet associated with pigment more or less commencing at Sc-R anastomosis but distinctly and consistently oblique to Sc, last nearly in line with R; FW pterostigma pigment distribution ill-formed, breadth about 1.5 times height; T2 and anterior half of t3 with an intermediately dense coat of medium length stiff black setae mixed with some medium long slender pale gray setae, coat with setae becoming short on posterior half of T3 to anterior half of T5, posterior half of T5 to T9 with setae dense, medium short, slender, stiff, black; pleural membrane setae of segments 1–2 with a very sparse coat of short slender black setae, these becoming denser on segments 3–8; T9 dorsal surface of males with some parts of lateral marginal surfaces cream or yellow; pulvini protruding well beyond margins of genital capsule in undissected specimens; GPC in lateral view smoothly arched from base to apex; GPC without a dorsal notch; parameres long acuminate tusks curving dorsad; pelta a slightly produced dorsoventral carina fused laterally with parameres; pulvini well-developed, more than four to eight times longer than width at base, bulb-like, bearing long stiff setae; abdominal tergite maculation present, but only as a diffuse darkness projecting anterad and posterad from tergal antecostal scar, which is usually colored pale yellow to white.

Discussion.—This species group was previously recognized as the genus *Ascaloptynx* Banks. Unmistakably monophyletic, it represents a highly derived lineage within *Haploglenius*. It was placed in the cladistic analysis as sister group to the *gerstaeckeri* species group (formerly *Verticillecerus* van der Weele), a relationship hypothesized by van der Weele (1909), but it shows affinities for the *flavicornis* species group in wing and pterostigma shape, and for *Haploglenius abdominevittatus* Ardila and Jones in wing shape, body setae coloration, verticils, and several other features. Ongoing molecular studies may be useful to corroborate the current placement or enable a more confident one.

At the species group level, the genitalia of the males are very distinct. Between the species they express some variability, but the differences, particularly of the GPC, are only very slight and difficult to characterize. The genitalia of females are essentially indistinguishable from one species to another.

Ascaloptynx oligocenicus Nel is removed from the group. See discussion for *oligocenicus* under 'Removed from *Ascaloptynx*', below.

Haploglenius appendiculatus ***(Fabricius, 1793) new combination***

(A3 Fig. 38–39, 86)

Ascalaphus appendiculatus Fabricius, 1793

—Fabricius 1793 r#2311: 96 {OD: sex not indicated (♀—see Shetlar 1977: 99). TS: not indicated [holotype by monotypy—see van der Weele 1909]. TL: indicated as unknown (by Fabricius and van der Weele 1909, but as “Carolinas” by Shetlar 1977). TR: BMNH. Type specimen examined (see “Type material examined” below).}

—Lefèbvre 1842.04.?? r#3666: 7 {TSP (of *Orphne* new genus, misidentification of *Ascalaphus macrocercus* Burmeister; see “*Position of Orphne Lefèbvre*” under “Discussion” below)}

—Rambur 1842.12.31 r#5314: 363 {SYN}

—Walker 1853 r#6194: 446 {D, GD, SYN}

—Hagen 1861.07.?? r#455: 327 {DIS, GD, L, SYN}

—Hagen 1866 r#460: 381 {L, SYN}

—McLachlan 1871.09.14 r#353: 234, 239 {DIS, SYN, TSP (of *Ptynx* Lefèbvre)}

—van der Weele 1909.01.05 r#420: 56 {SYN, TR, TS, TSP (of *Neuroptynx* McClendon)}

—Orfila 1949 1949 r#5020: 190 {DIS, SYN, TSP (of *Neuroptynx* McClendon)}

—Shetlar 1977 r#5727: 99 {Ph.D. dissertation, nomenclatural acts invalid: DIS, SYN, TSP (of *Neuroptynx* McClendon, conspecific with *Ptynx juvenilis* McLachlan)}

Ascalaphus appendiculatus Latreille [sic], 1793

—Banks 1915 r#68: 350 {TSP (of *Ascaloptynx* n. n.)}

—Penny 1982a r#5105: 398 {TSP (of *Ascaloptynx* Banks)}

—Nel 1991. ??.?? r#8267: 333 {L}

Orphne appendiculata (Fabricius, 1793)

—Lefèbvre 1842.04.?? r#3666: 7 {NC (misidentification of *Ascalaphus macrocercus* Burmeister; see "*Position of Orphne Lefèbvre*" under "Discussion" below)}

—Hagen 1866 r#460: 454 {L, JSYN (of *Haploglenius appendiculatus* (Fabricius)}

—Oswald and Penny 1991.12.02 r#7138: 10 {DIS, SYN, TSP}

Haploglenius appendiculatus (Fabricius, 1793)

—Rambur 1842.12.31 r#5314: 363 {DIS, GD, NC, RD: ♂, SYN}

—Hagen 1861.07.?? r#455: 327 {DIS, L, SYN}

—Hagen 1866 r#460: 406 {DIS, GD, L, SYN}

—McLachlan 1871.09.14 r#353: 239 {SYN}

—van der Weele 1909.01.05 r#420: 56 {SYN}

—Shetlar 1977 r#5727: 99 {Ph.D. dissertation, nomenclatural acts invalid: SYN}

Ptynx appendiculata (Fabricius, 1793)

—McLachlan 1871.09.14 r#353: 239 {GD, NC, RD: sex not indicated, SYN}

—McLachlan 1891 r#385: 510 {MOR}

—van der Weele 1909.01.05 r#420: 56 {SYN}

—Shetlar 1977 r#5727: 99 {Ph.D. dissertation, nomenclatural acts invalid: SYN}

Neuroptynx appendiculata (Fabricius, 1793)

—van der Weele 1909.01.05 r#420: 56, fig. 28 {GD, NC, RD: ♂♀, SYN, TR, TS}

—Froeschner 1947 r#2422: 129 {DIS, GD, K}

—Shetlar 1977 r#5727: 99, figs. 14a–d, 25a–d, 40 {Ph.D. dissertation, nomenclatural acts invalid: D, DIS, MOR, RD: ♂♀, SR, SYN, TR, TS}

—Lago and Testa 1989 r#3608: 12, figs. 1, 2 {BIO, DIS, GD, HAB, K, SR}

Ascaloptynx appendiculata (Fabricius, 1793)

—MacLeod 1964 r#3954: {Ph.D. dissertation, nomenclatural acts invalid: BIO, IMS, MOR}

—Henry 1976 r#2876: 2 {DIS}

—Henry 1977 r#2877: 182 {HAB, IMS}

—Shetlar 1977 r#5727: 99 {Ph.D. dissertation, nomenclatural acts invalid: SYN}

—Penny 1982a r#5105: 398 {L}

—Penny, Adams and Stange 1997.12.09 r#8867 {DIS, GD, L, SYN, TL, TR, TS}

Etymology and nomenclatural notes.—*appendiculatus*: appendicula (Latin), 'appendage, addition' + -atus (Latin), 'having the nature of': 'having an appendage'. Uncertain, but probably referring to the produced axillary angle of the FW.

Diagnosis.—Distal cells of costal area divided by oblique crossveins. Subcostal area tinged with brown color. Rs sometimes yellowish. Abdominal tergites 3-7 lacking maculations near antecostal scars, or if present, only a very diffuse spot around scar. S3 longitudinal black stripes posteriorly with diffuse margins, often fading before striking posterior transverse black stripe, which is narrow. Males: Pronotal valve not developed. Abdomen not extending past the wingtips in unspread specimens. T3 distal margin without a process, although sometimes a very small nub may be present.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Eastern U.S.: eastward from eastern Texas and Oklahoma.

Description.—

Size (mm). Male: length of body 33–47, abdomen 25–38, forewing 35–46, hind wing 34–42, antennae 21–25. Female: length of body 32–39, abdomen 25–29, forewing 40–47, hind wing 39–45, antennae 21–25.

Head. Occiput base color reddish brown, pattern consisting of irregular yellow or orange blotches positioned laterally and ventrally, these continuing onto vertex as lateral plates. Vertex somewhat swollen, somewhat bilobed, dark reddish brown with irregular yellow blotches; setae moderately dense to somewhat sparse, long, slender, somewhat wavy, mixed black and pale gray. Extra-torular sclerites concolorous with prefrons, orange to medium dark brown. Paraocular band narrowly dull dark brown laterad of antennae, otherwise yellow. Frons pale to orangish yellow, often narrowly and diffusely dark brown in dorsal third, bearing a diffuse, incomplete, reddish brown sagittal line, this sometimes reduced to a dorsal macula; setae moderately dense, white. Clypeus pale yellow, often slightly darkened laterally. Labrum concolorous with mesal portion of clypeus. Mandibles basally yellow, dark reddish brown apically. Labium pale amber yellow, with a thin dark reddish brown sagittal line, this sometimes incomplete or absent. Eyes very slightly dorsoventrally oblong. Antennae somewhat short, not reaching past third fork of Rs in spread specimens, flagellomeres slightly swollen at nodes, flagellum somewhat pale to dark reddish brown, flagellomeres often becoming darker in distal third, nodes thinly pale, internodes setose on distal two-thirds, setae denser in distal half of antenna, small, slender but robust, black, nodes also bearing slender black setae, these developed into verticils with length exceeding previous flagellomere on ca.

basal 6-7 flagellomeres, gradually shortening until a third or less of flagellomeres' length; clubs pyriform, brown, all surfaces covered in fine dark setae.

Thorax. Cervix. Dorsal cervical plate setae white. Cervical sclerite color variable, ventroapically dark brown, narrowly yellow dorsally and sometimes proximoanteriorly. Anterior flange a narrow collar, broadening posteromesally, weakly produced dorsad. Medial transverse band very narrow mesally. Posterior flange of females covering mesoacrotergite, in males covering mesoacrotergite to midpoint of anterior swelling of mesoprescutum, but not articulated or valve-like, white crystalline material absent. Pronotum base color dark brown, broad yellow or orange longitudinal stripes running sublaterally from anterior flange to posterior margin of posterior flange and often continuing onto pteronotum. All surfaces bearing long, somewhat slender, black setae with some medium long, wispy, pale yellow or white setae mixed in. *Pteronotum*. Evenly dark earthy brown, yellow maculations often, but not always, organized into sublateral longitudinal stripes running from lateral surface of mesoprescutum, posteriorly on scutum, onto scutellum; velvety spots of metascutum reddish brown; entire surface of pteronotum covered with moderately dense, long, slender, golden brown setae with numerous pale gray or white setae directed posterad on posterolateral surfaces of mesoscutum and posterior margin of mesoscutellum, metanotum largely covered with long, slender, white setae. *Pleuron* variegated brown and yellow, yellow coloration somewhat organized into a median longitudinal stripe, but this obscured by setae; pleural setae dense, long, wispy, white, entire pleuron often with pruinescence.

Legs. Leg color patterns somewhat variable, base color yellowish orange, femora dusky dark brown in proximal two thirds, tibiae often dusky reddish brown on anterolateral surfaces, remaining surfaces yellowish orange. Tarsi usually medium reddish brown, sometimes paler or darker, proximal margins dark brown and tarsi appearing annulated. Coxae setae pale yellow to white; femora with setae white, very short ventrally, very long laterally, and some long, somewhat slender, stiff, black setae mixed in on posterolateral surface, tibiae with numerous long, stiff, somewhat slender, black setae with numerous short and a few long, stiff, slender, white setae mixed in; antennal comb setae golden.

Wings. Dimension and shape. Somewhat long and slender, anterior and posterior margins subparallel in distal two-thirds, wings strongly narrowed at base, more so in HW, apices evenly rounded. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, width of cells more or less coequal to height, becoming slightly narrower in distal half of wing, distal costal cells often divided by oblique crossveins. Pterostigma small, with four to six forked and unforked brown veinlets, these sometimes narrowly margined with dark brown pigment; membrane colorless to slightly tinged with cream color, usually translucent but sometimes weakly opaque, distal margin of pigment, if present, fading evenly into apical area. Deltus devoid of pigment. Presectoral area with ca. nine to eleven cells. Rs with ca. seven to eight forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. twelve to fourteen irregular to more or less complete rows of cells. Cubital triangle distal domain with one to two cells. Anal area hind margin distinctly concave, anal angle well developed, elongate triangular and tooth-like, a single very narrow cell row distad of Cup + 1a. *Color and patterning.* Venation pale to dark brown, Rs sometimes yellowish. Costal area sometimes very lightly tinged with brownish color, subcostal area usually faintly tinged brown. Some specimens with entire wing membrane very weakly tinged with brown. HW. As in forewing except as follows. Mp_2 fork angle essentially 90°. Medial triangle distal domain absent. Pre-Cup axillary disk very pale, translucent. Pre-Mp_1 area margin greatly reduced, concave proximad of Mp_{2p}. Anal area with one very narrow but complete row of cells.

Abdomen. In males, usually extending nearly to wing apex when wings folded back; in females, not reaching to pterostigma. *Tergum*. T1 with mesal membrane expanded and plates somewhat reduced, T2 acrotergite somewhat elongate, coequal in length to T2, in males, in lateral view T2 and proximal half of T3 dorsally slightly arched or humped, posterior margin of T3 essentially undeveloped, sometimes very slightly produced into a tiny paired nub, remainder of abdomen narrowly cylindrical, in females abdomen not narrow; more or less evenly dull reddish brown, an orange maculation usually surrounding each antecostal scar, this flanked anteriorly and posteriorly by a broad area of diffuse black pigment, this continuing posterad and forming a diffuse broad, transverse band just anterad of posterior margin, posterior margin often narrowly yellow or orange; T1 to T3 with moderately dense, long, somewhat slender, mixed black and white setae, these transitioning to somewhat short, slender, stiff black setae along entire tergum. *Sternum*. Base color very dark brown to black, S1 anteromesally dark, otherwise yellowish, S2 yellowish with mesal membrane dark, S3 anterior margin transversely pale yellow, a sublateral pale yellow stripe running longitudinally posterad, often becoming diffuse in distal third, another narrow yellow stripe positioned laterad and running toward hind margin, a broad transverse yellow stripe positioned just anterad of posterior margin, posterior margin narrowly dark brown to black, this pattern repeated on S4 and S5, and sometimes on S6, remaining sternites more or less evenly brown, but often with dark longitudinal stripes; some long, wispy, pale yellow setae on S2, remaining surfaces of sternites with somewhat numerous, somewhat short, slender, stiff, black setae. *Pleural membrane*. Dark brown, often with irregular yellow maculations; devoid of long setae.

Male terminalia. Unmacerated specimens. GPC everted, parameres sclerotized, dark reddish brown, produced as dorsolaterally curving tusks, these joined mesally by pelta, which is expressed as a sagittal carina, tusks partially hidden laterally by pulvini, pulvini long, reddish brown, produced distad, apically bulbous, with numerous long, stiff, slender, black setae, ectoprocts simple, orangish yellow, and S9 reddish brown, apically paler. *Macerated specimens.* S9 apical margin essentially straight. Pulvini greatly produced, length ca. five times longer than width at base, with some small slender setae dorsally near base. GPC proximodorsal surface with some very small, slender, pale brown setae. Parameres proximodorsally carinate, carina produced dorsally into an irregular ridge, with teeth poorly defined. Pelta very narrow, elongate, sclerotized.

Female terminalia. Unmacerated specimens. Ventrovalvae dull yellowish brown, distivalvae and ectoprocts pale yellowish brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views very elongate and narrow, length ca. three and a half to four times width. Linguella weakly differentiated from surrounding membrane, bearing several short, robust, slender, black setae. Interdental space small, more or less round. Interdens absent.

Variation. Notal patterns of thorax variable, sometimes forming into stripes, but these only partially complete and diffuse. Tergal patterns of abdomen variably expressed, but dark maculations flanking antecostae not usually forming into distinct triangles.

Type material examined.—Examined briefly, but specimen not borrowed for this study and no JRJ database label applied.

Additional material examined.—*USA*: Alabama (FMNH: 1 ♀, JRJ_01319; TAMU: 1 ♂, JRJ_01550, 3 ♀♀, JRJ_01499, JRJ_01516, JRJ_01564; UMMZ: 1 ♂, JRJ_01318); Arkansas (CMNH: 1 ♂, JRJ_01308; MSUC: 1 ♀, JRJ_01309; TAMU: 3 ♂♂, JRJ_01527, JRJ_01537, JRJ_01589, 2 ♀♀, JRJ_01583, JRJ_01586; UMRM: 1 ♂, JRJ_01310); Florida (BYUC: 1 ♀, JRJ_01359; CMNH: 2 ♀♀, JRJ_01339, JRJ_01351; EMEC: 1 ♂, JRJ_01346; SEMC: 1 ♂, JRJ_01349; TAMU: 1 ♂, JRJ_01518, 3 ♀♀, JRJ_01505, JRJ_01512, JRJ_01535; UCDC: 1 ♂, JRJ_01347; UMMZ: 3 ♂♂, JRJ_01348, JRJ_01350, JRJ_01354, 5 ♀♀, JRJ_01353, JRJ_01355, JRJ_01357, JRJ_01358, JRJ_01360; UMRM: 1 ♀, JRJ_01356); Georgia (UMMZ: 1 ♀, JRJ_01345); Illinois (TAMU: 1 ♀, JRJ_01528); Louisiana (TAMU: 4 ♀♀, JRJ_01524, JRJ_01525, JRJ_01572, JRJ_01600); Mississippi (JRJC: 1 ♂, JRJ_10175); Missouri (UMMZ: 1 ♀, JRJ_01314; UMRM: 2 ♂♂, JRJ_01316, JRJ_01317, 5 ♀♀, JRJ_01311, JRJ_01312, JRJ_01313, JRJ_01315, JRJ_01611); North Carolina (BYUC: 2 ♂♂, JRJ_01343, JRJ_01344); Oklahoma (TAMU: 3 ♂♂, JRJ_01551, JRJ_01560, JRJ_01570, 2 ♀♀, JRJ_01554, JRJ_01557); South Carolina (SDMC: 1 ♂, JRJ_01609, 1 ♀, JRJ_01608); Tennessee (EMUS: 1 ♀, JRJ_01326; FMNH: 3 ♂♂, JRJ_01335, JRJ_01337, JRJ_01338, 13 ♀♀, JRJ_01320, JRJ_01321, JRJ_01322 (A3 Fig. 39), JRJ_01323, JRJ_01325, JRJ_01328, JRJ_01329, JRJ_01330, JRJ_01332, JRJ_01333, JRJ_01334, JRJ_01336, JRJ_01612; MSUC: 1 ♀, JRJ_01331; 2 ♀♀, JRJ_01324, JRJ_01327); Texas (BYUC: 1 ♂, JRJ_01495; JRJC: 1 ♂, JRJ_01544 [A3 Fig. 38]; TAMU: 5 ♂♂, JRJ_01497, JRJ_01529, JRJ_01534, JRJ_01568, JRJ_01574, 8 ♀♀, JRJ_01541, JRJ_01545, JRJ_01558, JRJ_01569, JRJ_01580, JRJ_01581, JRJ_01598, JRJ_01599; UMRM: 1 ♂, JRJ_01496); Virginia (CMNH: 1 ♂, JRJ_01340, 1 ♀, JRJ_01342; USNM: 1 ♂, JRJ_01341, 1 ♀, JRJ_01610); locality uncertain (MFNB: 1 ♀, JRJ_01519. TAMU: 2 ♀♀, JRJ_01520, JRJ_01539. UMMZ: 1 ♂, JRJ_01352).

Morphology, biology and ecology.—The physical attributes, life cycle and biology of the larvae and other life stages are probably very similar to that of *juvenilis*, described by Henry (1972, 1976, 1977, 1978a, 1978b) for *juvenilis* (as *furciger*). However, Henry (1977) reports that *juvenilis* larvae in Arizona reside in leaf litter, but notes that Peterson (1953) stated he swept larvae of *appendiculatus* from foliage of trees and bushes in Ohio.

This species is one of two haplogleniines known to occur regularly in the U.S., and I have made a few direct observations of individuals in the field. As with many other owlflies (e.g., *Ululodes*), the adults fly swiftly at dusk, and individuals are occasionally captured at or near MV lights, but they do not seem to be attracted to them, and they have not been observed to alight upon a light sheet (although one did hover briefly in front of an MV lamp). They are rare in many habitats and more frequently encountered in others, but not in great numbers. They do not make as sharp turns in the air as do *Ululodes* spp.

Discussion.—Shetlar (1977) examined specimens of *Neuroptynx* and decided they constituted one continuously varying species. He synonymized them under *appendiculatus*, an act later made valid by Penny et al. (1997). In particular, Shetlar looked at the male T3 process and characterized it as occurring in several states, namely a slight hump, a hump with bristles, a short entire hump, a short divided hump, a medium divided hump, a long thin divided hump, and a long thick divided hump. Over 300 specimens, including over 130 males, were examined in this study, and it was found that while there is considerable variation in the length and robustness of the process when it occurs, it is essentially present or absent. When present it may be short or long, unforked, briefly forked or deeply forked, very thin to more robust, and with setae short to very long. When 'absent', it is usually completely unexpressed, but sometimes occurs as a tiny nub on the posterior margin, this sometimes barely divided, but hardly longer than portions of a millimeter, and rarely with setae. This condition is interpreted to be incipient. When this revised characterization of presence/absence is made, plotting the two phenotypes on a map (A3 Fig. 86) shows a clear division in the distribution of the states, with individuals lacking a process occurring in east Texas and eastward, and those with some form of a process occurring in central Texas and westward. The geographic division is linear, with dozens of specimens of each type occurring on either side of the line without overlap. This striking separation appears to indicate some form of mutual exclusion, perhaps climatically adaptive or possibly competitive. Subsequent careful examination of loan material revealed several additional diagnostic features (many rather subtle) that appear to correspond with species-level differentiation of two groups, and these groupings are determined here to represent two independent species. Additional corroboration of the independence of the lineages was observed in genetic distance of molecular sequence data (unpublished data).

Haploglenius juvenilis *(McLachlan, 1871) new status, new combination*

(A3 Figs. 40–41, 86)

Ptynx juvenilis McLachlan, 1871

—McLachlan 1871.09.14 r#353: 239 {OD: not indicated [♂], D, DIS. TS: not indicated [holotype by monotypy]. TL: “Texas” (USA). TR: indicated as McLachlan personal collection (BMNH). Type specimen examined (see “Type material examined” below).}

—McLachlan 1891 r#385: 510 {DIS, GD, MOR}

—McClendon 1906.05.?? r#3839: 172 {GD, L (under *Neuroptynx* new replacement name, for *Ptynx* Lefèbvre, 1842)}

—van der Weele 1909.01.05 r#420: 58 {DIS, MOR, SYN, TR, TS}

—Shetlar 1977 r#5727: 99 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus appendiculatus* Fabricius)}

—Penny, Adams and Stange 1997.12.09 r#8867:42 {JSYN (of *Ascalaphus appendiculatus* Fabricius), TL, TR, TS}

Neuroptynx juvenilis (McLachlan, 1871)

—van der Weele 1909.01.05 r#420: 58, figs. 29, 30 {D, DIS, MOR, SR, TR, TS}

—Shetlar 1977 r#5727: 99 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus appendiculatus* Fabricius)}

Ascaloptynx juvenilis (McLachlan, 1871)

—Penny 1982a r#5105: 398 {L}

—Nel 1991. ??.?? r#8267: 333 {L}

Ptynx furciger McLachlan, 1891

—McLachlan 1891 r#385: 509 {OD: ♂♀, D, DIS, MOR. TS: syntypes, 3 ♂♂, 2 ♀♀ [a lectotype needs to be designated from syntype material]. TL: “Arizona” (USA). TR: indicated as McLachlan personal collection (BMNH). Type specimen examined (see “Type material examined” below).}

—van der Weele 1909.01.05 r#420: 59 {SYN, TL, TR, TS}

—Penny, Adams and Stange 1997.12.09 r#8867:42 {JSYN (of *Ascalaphus appendiculatus* Fabricius), TL, TR, TS}

Neuroptynx furciger (McLachlan, 1891)

—van der Weele 1909.01.05 r#420: 58, figs. 31, 32 {D, GD, MOR, RD: ♂♀, SYN, TL, TR, TS}

Ascaloptynx furciger (McLachlan, 1891)

—Henry 1972 r#2875: 1–22, figs. 1, 3B, 5A, 7, 8, 9, table 1 {BIO, DIS, EVO, IMS, MOR}

—Henry 1976 r#2876: 1–31, figs. 5-7 {BIO, DIS, EVO, IMS, MOR}

—Henry 1977 r#2877: 179–195, figs. 3, 10, table 2 {BIO, DIS, EVO, IMS, MOR}

—Henry 1978a r#2880: 10, 12, 17, table 3 {BIO, DIS, IMS, MOR}

—Henry 1978b r#2878: 75, 76, table 1 {BIO, DIS, IMS, MOR}

—Nel 1991. ??.?? r#8267: 333 {L}

—Tjeder 1992 r#7246: 33 {BIO}

Ascalopteryx [sic] *furciger* (McLachlan, 1891)

—Tjeder 1992 r#7246: 56 {DIS, IMS, ISS}

Etymology and nomenclatural notes.—*juvenilis*: juvenilis (Latin), ‘of youth’. In reference to the perceived diminutive size of the type specimen relative to other species known at the time.

Diagnosis.—Distal cells of costal area undivided by oblique crossveins. Subcostal area tinged with brown color. Abdominal tergites 3-7 with diffuse to well-defined often triangular black maculae, these positioned both anterior and posterior to tergal lateral antecostal scars. S3 black longitudinal stripes with well-defined edges along entire length. Males: Pronotal valve not developed. Abdomen not extending past the wingtips in unspread specimens. Distal margin of T3 bearing an erect elongate process, this highly variable in size and shape, but often slender with a forked apex.

Autapomorphies.—T2–T3 with an moderately sparse coat of medium length, slender yellow or golden setae, this becoming progressively sparser and shorter distally, T4–T9 blending from short slender golden setae to short slender stiff black setae; abdominal tergite maculation present, a more or less well-developed dark triangular macula projecting anterad and posterad from tergal fascia, which is usually colored pale yellow to white.

Distribution.—U.S.: central Texas and Oklahoma west; northwestern Mexico.

Description.—

Size (mm). Male: length of body 34–42, abdomen 26–33, forewing 31–40, hind wing 30–39, antennae 19–20. Female: length of body 27–44, abdomen 18–33, forewing 37–45, hind wing 36–44, antennae 18–24.

As in *appendiculatus*, except as follows:

Head. Occiput reddish brown near cervical membrane, laterally and dorsally almost completely dull yellow, this continuing onto vertex. Extra-torular sclerites concolorous with upper portion of frons, orange to medium dark brown. Paraocular band often narrowly brown along lateral margins of frons. Antennae not reaching past second fork of Rs in spread specimens, flagellum somewhat pale to dark yellowish or reddish brown, verticils with length exceeding previous flagellomere on ca. basal 6-10 flagellomeres.

Thorax. Cervix. Dorsal cervical plate setae pale yellow.

Legs. Femora pale to dark dusky reddish brown, a narrow yellow stripe present on distal two-thirds of dorsal surface, tibiae dusky dark reddish brown, narrowly yellow in proximal two-thirds of dorsal surface. Coxae setae white; antennal comb setae pale golden.

Wings. Dimension and shape. Pterostigma very small; membrane colorless to slightly tinged with cream or pale brown color, not filling pterostigma cells. Presectoral area with ca. nine to ten cells. Cubital area with ca. eleven to thirteen irregular to more or less complete rows of cells.

Abdomen. Tergum. Posterior margin of T3 distinctly produced mesally into a narrow, fluted, apically bifurcate process, anterior surface bearing numerous long, slender, black setae; integument more or less evenly grayish brown, area around antecostal scar pale, this area flanked anteriorly and posteriorly by a usually distinct, elongate, triangular black macula. *Sternum*. S3 mesally bisected by medium black stripe, sublateral pale yellow stripe margins well formed and distinct along entire length, yellow stripe positioned laterad and running toward hind margin with margins also well formed and distinct, posterior margin broadly dark brown to black, this pattern often repeated on all remaining sternites but becoming more diffuse distally; setae on S2 mixed with some moderately long, stiff, slender black setae. *Pleural membrane*. Dark grayish brown.

Male terminalia. Unmacerated specimens. S9 orangish yellow. *Macerated specimens.* Pulvini length ca. four to five times longer than width at base.

Female terminalia. Unmacerated specimens. Ventrovalvae, distivalvae and ectoprocts yellowish, ventrovalvae often laterally dark brown, sometimes becoming completely dark reddish brown. *Macerated specimens.* Ventrovalvae narrower proximally and broader distally, length more than four times width. Distivalvae in lateral view somewhat elongate ovoid. Interdental space elongate triangular.

Variation. Posterodorsal process of T3 highly variable; in most specimens the process is at least three to four times longer than width at base; however, the process can be shorter or longer, slightly broader or more narrow, and the apical bifurcation can be very well expressed or almost absent. Notal stripes variable as in *appendiculatus*, perhaps more frequently well developed into stripes. Dorsal maculae of abdominal rather variable, sometimes diffuse and resembling those of *appendiculatus*, but usually at least somewhat distinctly triangular. Some males are rather small, and on the whole *juvenilis* individuals are smaller than those of *appendiculatus*.

Type material examined.—*Holotype* of *Ptynx juvenilis*, male, USA, in BMNH collection: “Type /// Texas /// Type /// McLachlan Coll. B.M. 1938-674 /// Ptynx juvenilis, M. L. /// juvenilis McL. /// JRJ_01623”. Condition: Good, antennae and wings spread, abdomen missing, right HW tip dinged. *Holotype* of *Ptynx furciger*, male, USA, in BMNH collection: “Type /// McLachlan Coll. B.M. 1938-674 /// Type /// Arizona /// Ptynx furciger, ML. /// JRJ_01622”. Condition: Excellent, antennae and wings spread, no parts missing.

Additional material examined.—*Mexico*: Guerrero (TAMU: 2 ♀♀, JRJ_01372, JRJ_01373); Jalisco (SDMC: 2 ♀♀, JRJ_01369, JRJ_01370); Monterrey (TAMU: 1 ♂, JRJ_01362); Morelos (EMEC: 1 ♂, JRJ_01364); Nayarit (EMEC: 2 ♂♂, JRJ_01363, JRJ_01365, 1 ♀, JRJ_01367; SDMC: 2 ♀♀, JRJ_01366, JRJ_01368); San Luis Potosi (MFNB: 1 ♀, JRJ_01371); Sinaloa (EMEC: 1 ♂, JRJ_01361). *USA*: Arizona (BYUC: 8 ♂♂, JRJ_01378, JRJ_01386, JRJ_01390, JRJ_01403, JRJ_01405, JRJ_01406, JRJ_01408, JRJ_01447, 10 ♀♀, JRJ_01426, JRJ_01431, JRJ_01433, JRJ_01437, JRJ_01446, JRJ_01456, JRJ_01458, JRJ_01462, JRJ_01463, JRJ_01469; CMNH: 3 ♂♂, JRJ_01443, JRJ_01509, JRJ_01510, 1 ♀, JRJ_01417; EMEC: 4 ♂♂, JRJ_01388, JRJ_01396, JRJ_01427, JRJ_01428, 20 ♀♀, JRJ_01410, JRJ_01412, JRJ_01424, JRJ_01430, JRJ_01434, JRJ_01435, JRJ_01438, JRJ_01439, JRJ_01440, JRJ_01448,

JRJ_01449, JRJ_01450, JRJ_01451, JRJ_01452, JRJ_01453, JRJ_01454, JRJ_01464, JRJ_01465, JRJ_01467, JRJ_01468; EMUS: 1 ♀, JRJ_01445; FMNH: 1 ♀, JRJ_01415; JRJC: 3 ♂♂, JRJ_01513 [A3 Fig. 40], JRJ_01531, JRJ_10265; MFNB: 1 ♂, JRJ_01498, 3 ♀♀, JRJ_01413, JRJ_01416, JRJ_01419; MSUC: 1 ♂, JRJ_01511; SDMC: 13 ♂♂, JRJ_01376, JRJ_01377, JRJ_01379, JRJ_01380, JRJ_01381, JRJ_01382, JRJ_01383, JRJ_01384, JRJ_01385, JRJ_01391, JRJ_01411, JRJ_01603, JRJ_01606, 10 ♀♀, JRJ_01420, JRJ_01421, JRJ_01423, JRJ_01436, JRJ_01455, JRJ_01457, JRJ_01459, JRJ_01460, JRJ_01466, JRJ_01604; TAMU: 5 ♂♂, JRJ_01393, JRJ_01407, JRJ_01409, JRJ_01461, JRJ_01523, 6 ♀♀, JRJ_01414, JRJ_01543, JRJ_01547, JRJ_01552, JRJ_01573, JRJ_01605; UCDC: 2 ♂♂, JRJ_01394, JRJ_01400, 3 ♀♀, JRJ_01422, JRJ_01429, JRJ_01432, UMMZ: 2 ♂♂, JRJ_01401, JRJ_01507, 1 ♀, JRJ_01444); New Mexico (SDMC: 1 ♀, JRJ_01441; UDCC: 1 ♂, JRJ_01399, 2 ♀♀, JRJ_01425, JRJ_01442); Oklahoma (CMNH: 1 ♀, JRJ_01494; EMEC: 1 ♂, JRJ_01493; SEMC: 1 ♂, JRJ_01607; UMSP: 1 ♀, JRJ_01492); Texas (BYUC: 7 ♂♂, JRJ_01470, JRJ_01471, JRJ_01472, JRJ_01473, JRJ_01474, JRJ_01475, JRJ_01477, 9 ♀♀, JRJ_01480, JRJ_01481, JRJ_01482, JRJ_01483, JRJ_01484, JRJ_01485, JRJ_01486, JRJ_01487, JRJ_01488; EMEC: 9 ♂♂, JRJ_01387, JRJ_01389, JRJ_01392, JRJ_01395, JRJ_01397, JRJ_01398, JRJ_01402, JRJ_01404, JRJ_01476; JRJC: 1 ♂, JRJ_01514, 3 ♀♀, JRJ_01490, JRJ_01532 [A3 Fig. 40], JRJ_10014; SDMC, 1 ♀, JRJ_01491; TAMU: 28 ♂♂, JRJ_01501, JRJ_01506, JRJ_01515, JRJ_01521, JRJ_01522, JRJ_01533, JRJ_01536, JRJ_01538, JRJ_01540, JRJ_01542, JRJ_01546, JRJ_01548, JRJ_01555, JRJ_01561, JRJ_01565, JRJ_01566, JRJ_01571, JRJ_01576, JRJ_01577, JRJ_01578,

JRJ_01582, JRJ_01588, JRJ_01590, JRJ_01591, JRJ_01594, JRJ_01595, JRJ_01596, JRJ_01597, 14 ♀♀, JRJ_01517, JRJ_01526, JRJ_01530, JRJ_01549, JRJ_01553, JRJ_01556, JRJ_01559, JRJ_01562, JRJ_01563, JRJ_01567, JRJ_01575, JRJ_01579, JRJ_01584, JRJ_01592; UCDC: 1 ♂, JRJ_01479, 1 ♀, JRJ_01489; UMMZ: 1 ♀, JRJ_01478); locality unknown (TAMU: 1 ♂, JRJ_01508).

Morphology, biology and ecology.—Henry (1972, 1976, 1977) reared to third instar, from egg masses he collected in the vicinity of the AMNH Southwestern Research Station in Portal, AZ, larvae of *juvenilis* (as *Ascaloptynx furciger*), describing each pre-imaginal life stage and reporting biological data for the same. He also presented extensive information on the biology and habits of adults (1977). His work, along with that performed in the same papers for the sympatric species *Ululodes mexicanus*, represents the most comprehensive species-level treatment of the ecology of any owlfly species. A brief summary of his findings for *juvenilis* is provided here.

Adults are active in southeastern Arizona from early June to early September, with males becoming less abundant in the latter half of this period. Oviposition peaks in August. Eggs are laid in the semi-shaded foothills of mountains on vertical dead stems of perennials or grass clumps which are littered below with dry oak debris. Approximately 35 to 45 eggs are attached transversely by their midsections in parallel spiraling clumps. Repagula laid immediately below the main egg clump resemble small eggs and lack a fluid coating; these serve as food sources for freshly emerged larvae. Larvae, which are able to defend themselves from wasps and other invaders via mass head rearing and jaw snapping, remain on the twig for seven to ten days, and then walk to the ground and disperse. Larvae pass through three instars. They have a flat, square head, unique scale-like dorsal dolichasters, and short, dorsoventrally flattened, scolus-like processes in a common horizontal plane; the entire body is flattest marginally, but is not necessarily prominently flattened in the center of the abdomen when mature. They live in leaf litter but do not litter their dorsum with debris. They can open their jaws to 180°. Larvae are opportunistic sit and wait predators that rapidly grab and envenomate prey with their jaws by injecting a paralyzing agent. Once immobilized, the prey item will be fed upon for an hour or so. Larvae exhibit complex feeding and jaw cleaning behaviors. First and second larval instars last, on average, 34 and 32 days, respectively. Third instars reach full size at 30 days, but could not be induced by Henry to pupate. Tjeder (1992: 56) hypothesized they had entered diapause and probably hibernation.

Adults are active after sunset. Their flight is powerful and swift, but their feeding habits and prey unknown. In the lab, individuals "consistently subdued and consumed live 25 mm asilid flies that were hand fed to them". In the field, both sexes rest on grass stems or twigs with the heads down and abdomen projecting nearly perpendicular. The role of the long antennae are not yet well-understood (all Henry 1972, 1976, 1977).

A few notes can be added here from personal observations. Adult specimens are often captured at or near lights. They are swift flyers, sometimes seen cruising at dusk, and they occasionally alight on a light sheet, unlike *appendiculatus*. Like most owlflies, perhaps, *juvenilis* is rare in many habitats but frequently encountered in others, at certain times of the year.

Discussion.—Though not indicated in the original description, the type specimen of *juvenilis* is a male. From comments made later by McLachlan (1891), it seems that he was unsure of the sex of the specimen or its abdominal attributes at the time he described it in 1871 (he reported the abdomen missing in 1891, as it is today), and only received such information about the species secondarily from communications with Dr. Hagen (McLachlan 1891: 510). McLachlan, in describing *furciger*, reported that Hagen made no indication of a process on the third tergite in a male of *juvenilis* he examined from Texas, and this confirmed to McLachlan that *juvenilis* individuals must, then, lack such a process. Hagen certainly had a male of *appendiculatus*.

McLachlan (1871) made explicit that *juvenilis* was distinct from *appendiculatus* because of its small size. Although it is true that *juvenilis* individuals are generally smaller than those of *appendiculatus*, the differences are slight, and, in fact, it is a comparison between males and females where the greatest disparity is seen. It seems that McLachlan (1871), in describing *juvenilis*, was comparing his male, which specimen is a rather small individual when compared to other male conspecifics, to measurements for the type of *appendiculatus*, which is a female (see Shetlar 1977).

In the holotype of *juvenilis* the wings are smaller and slightly darker than in the holotype of *furciger*; the *juvenilis* specimen has poorly formed pteronotal stripes, whereas in *furciger* they are well developed; the legs are also darker in *juvenilis*. All of these features, however, vary somewhat continuously among large numbers of individuals, although pteronotal stripes and paler legs were more frequently (but not always) found in individuals from Arizona and Mexico, and specimens with poorly formed stripes or spots often were seen in specimens from central Texas and Oklahoma.

The origin of the *juvenilis* holotype is only indicated as "Texas (Belfrage)" ["Belfrage" refers to the collector, not a place, as suggested in Penny et al. 1997], but it must be central or western Texas; the geographic divide between *appendiculatus* and *juvenilis* runs through eastern Texas and Oklahoma (A3 Fig. 86) at ca. 96° longitude.

Haploglenius elongatus *new species*

(A3 Fig. 42, 86)

Etymology and nomenclatural notes.—*elongatus*: elongatus (Latin), 'prolonged'. Named for abdomen of males which extends past the wingtips in unspread specimens.

Diagnosis.—Wings very narrow, devoid of pigment (including subcostal areas). Distal costal cells not divided by oblique crossveins. T3 with dark maculations diffuse, usually indistinct. Males: Pronotal valve developed but small, articulable. Abdomen extending past the wingtips in unspread specimens. T3 distal process absent. Base color of sternites brown and not black. Female: Unknown.

Autapomorphies.—clypeus without dorsolateral maculation; male FW subcostal area devoid of pigment; male abdomen length extending beyond apex of wings folded over tergum.

Distribution.—Honduras; Mexico: Yucatan.

Description.—

Size (mm). Male: length of body 40–47, abdomen 34–39, forewing 35–38, hind wing 33–37, antennae 21–22.

Head. Occiput base color reddish brown, pattern consisting of irregular yellow or orange blotches positioned laterally and ventrally, these continuing onto vertex as lateral plates. Vertex very slightly swollen, not bilobed, dark reddish brown with irregular yellow blotches; setae moderately dense to somewhat sparse, long, slender, somewhat wavy, mixed black and pale gray. Extra-torular sclerites concolorous with frons. Paraocular band narrowly dull dark brown near antennae, otherwise yellow. Frons pale to orangish yellow, bearing a diffuse, incomplete, reddish brown sagittal line, this sometimes reduced to a dorsal macula; setae moderately dense, white. Clypeus pale yellow, sometimes slightly darkened laterally. Labrum concolorous with mesal portion of clypeus. Mandibles basally yellow, dark reddish brown apically. Labium pale yellow, with a thin dark reddish brown sagittal line. Eyes very slightly dorsoventrally oblong. Antennae somewhat short, not reaching past third fork of Rs in spread specimens, flagellomeres slightly swollen at nodes, flagellum somewhat pale reddish or yellowish brown, nodes sometimes thinly pale, internodes setose on distal two-thirds, setae small, slender but robust, black, nodes also bearing slender black setae, these developed into verticils with length exceeding previous flagellomere on ca. basal 10 flagellomeres, gradually shortening until about half flagellomeres length; clubs pyriform, brown, all surfaces covered in fine dark setae.

Thorax. Cervix. Dorsal cervical plate setae white. Cervical sclerite apically yellow, subapical surface to base variable, yellow to dark brown. Anterior flange a narrow collar, broadening mesoposteriorly to touch posterior flange, weakly produced dorsad. Medial transverse band mesally obliterated by anterior flange. Posterior flange valve-like, overlapping acrotergite posterad of midpoint of anterior swelling of mesoprescutum, ventral surface with coating of white crystalline material. Pronotum base color dark brown, sublaterally pale brown, orange, or yellowish. All surfaces bearing long, somewhat slender, black setae with some medium long, wispy, pale yellow or white setae mixed in. *Pteronotum*. Dark earthy brown, diffusely yellow on lateral surfaces of anterior swelling and posteromesal surface of mesoprescutum, posterad of wing base on posterolateral surface of mesoscutum, and transversely just anterad of posterior swelling of mesoscutellum, posterior surface sometimes with sublateral diffuse dark brown coloration; velvety spots of metascutum pale reddish brown, inconspicuous;

entire surface of pteronotum covered with moderately dense, long, slender, black setae with numerous pale gray or white setae directed posterad on posterolateral surfaces of mesoscutum and posterior margin of mesoscutellum. *Pleuron* with sclerites mostly yellow, sometimes variegated with small areas of diffuse brown color; pleural setae dense, long, wispy, white, entire pleuron with pruinescence.

Legs. Leg color patterns somewhat variable, base color yellowish orange, femora dusky dark brown in apical half, this darkest on posterolateral surfaces of pro- and mesothoracic legs, tibiae yellow ventrally and in a narrow stripe on proximal half of dorsal surface, yellow color sometimes broadening mesally. Tarsi medium to dark reddish brown, apical tarsomere pale at apex. Coxae setae white; femora with setae white, very short ventrally, very long laterally, and some long, somewhat slender, stiff, black setae mixed in on posterolateral surface, tibiae with numerous long, stiff, somewhat slender, black setae with numerous short and a few long, stiff, slender, white setae mixed in; antennal comb setae golden.

Wings. Dimension and shape. Somewhat long, very slender, especially HW, wings strongly narrowed at base, more so in HW, apices evenly rounded. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, width of cells more or less coequal to height. Pterostigma small, with four to six forked and unforked brown veinlets, these often narrowly margined with dark brown pigment; membrane colorless to slightly tinged with cream color, usually translucent but sometimes weakly opaque, distal margin of pigment, if present, fading evenly into apical area. Deltus devoid of pigment. Presectoral area with ca. nine to eleven cells. Rs with ca. six to seven forks.

$Mp_2 + Cua_1$ evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. thirteen irregular to more or less complete rows of cells. Cubital triangle distal domain with one to two cells. Anal area hind margin distinctly concave, anal angle well developed, triangular and tooth-like, a single very narrow cell row distad of Cup + 1a. *Color and patterning.* Venation pale to dark brown. Costal area sometimes very lightly tinged with brownish color, wings otherwise devoid of pigment. Some specimens with entire wing membrane very weakly tinged with brown. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain absent. Pre-Cup axillary disk very pale, translucent. Pre-Mp_1 area margin greatly reduced, concave proximad of Mp_{2p}. Anal area with one complete row of cells.

Abdomen. Usually extending beyond apex of wings when folded back. *Tergum*. T1 with mesal membrane expanded and plates somewhat reduced, T2 acrotergite somewhat elongate, nearly coequal in length to T2, in lateral view T2 and proximal half of T3 dorsally arched or humped, remainder of abdomen narrowly cylindrical; more or less evenly dull reddish brown, a diffuse orange maculation sometimes surrounding each antecostal scar, a diffuse brown macula sometimes positioned anterad and usually another immediately posterad, this transitioning to a diffuse cinnamon to orange colored stripe continuing posterad almost to hind margin of tergite; T1 to T3 with moderately dense, long, somewhat slender, mixed black and white setae, these transitioning to somewhat short, slender, stiff black setae along entire tergum. *Sternum*. Base color medium to dark brown, S1 often predominately yellow, mesally brown, with a narrow dark brown sagittal stripe, S2 mesally brown, laterally yellow, also with a narrow dark brown sagittal stripe, S3 with a sublateral longitudinal yellow stripe, this becoming narrower and diffuse distad and not joining hind margin of sternite, a narrow, well defined, transverse yellow band positioned just anterad of posterior margin of S3 to S5, and sometimes on more distal sternites; some long, wispy, pale yellow setae on S2, remaining surfaces of sternites with somewhat numerous, somewhat short, slender, stiff, black setae. *Pleural membrane*. Dark brown, often with irregular yellow maculations, devoid of long setae.

Male terminalia. *Unmacerated specimens.* GPC distinctly everted, parameres sclerotized, dark reddish brown, mesally pale yellow, produced as dorsolaterally curving tusks, these joined mesally by pelta, which is expressed as a sagittal carina, pulvini extremely long, ventromesally membranous, pale yellow, apically dark reddish brown, produced laterodistad, apically bulbous, with numerous long, stiff, slender, black setae, ectoprocts simple, brownish yellow, and S9 reddish brown, apically paler.

Macerated specimens. S9 apical margin essentially straight. Pulvini greatly produced, length ca. six to eight times longer than width at base, with some small slender setae near base. GPC proximodorsal surface with some very small, slender, pale brown setae. Parameres proximodorsally carinate, carina produced into two or three small, sharp, irregular teeth. Pelta very narrow, sclerotized.

Variation. In dried specimens, the pulvini are sometimes held laterad and sometimes directed distad. Intensity of the coloration on the thorax and abdomen varies somewhat, and the abdominal pattern varies from somewhat obscure to fairly well expressed.

Type material examined.—*Holotype* (A3 Fig. 42), **new designation**, male, Honduras, in FSCA collection: “HONDURAS: El Paraiso Yuscaran, (Rio Aguacote), 2800' 29-IV-1993 L. Stange & R.Miller /// Neuroptynx appendiculatus (Fab.) det L. Stange '93 /// HOLOTYPE Haploglenius elongatus Jones ♂ design. J. R. Jones 2014 /// JRJ_01602”. Condition: excellent; antennae and wings spread, no parts missing, wing posterior margins with a few small dings.

Additional material examined.—*Honduras*: Francisco Morazan (FSCA: 1 ♂, JRJ_01601). *Mexico*: Yucatan (EMEC: 1 ♂, JRJ_01374; TAMU: 1 ♂, JRJ_01375).

Morphology, biology and ecology.—One specimen was collected at light.

Discussion.—Though this species has the distinctive verticillate antennae, body setosity, pleuron patterning, wing shape, slender abdomen, and male genitalia seen in *appendiculatus* and *juvenilis*, it retains many plesiomorphic traits of other NWH (e.g., presence of the pronotal valve in males, distal costals undivided, base color of the sternum brown, tergal and sternal patterns only weakly developed, etc.). As expected it was placed basad of *appendiculatus* and *juvenilis* in the cladistic analysis. The only known specimens of *elongatus* occur in northern Central America, whereas *juvenilis* only occurs in Mexico and the western U.S., and *appendiculatus* has only been reported from the eastern U.S. These clues collectively suggest an invasion of North America by the *appendiculatus* species group from Central American *elongatus*–like ancestors.

reticulatus *species group*

Diagnosis.—*Head*. Antennae long, flagellomeres distinctly swollen at nodes, nodes pale, clubs elongate, apices at least weakly acuminate. *Thorax*. In males, pronotal valve developed or not. Mesacrotergite not produced. Pleuron with a somewhat variegated appearance, paired oblique pale stripes weakly formed to absent. *Wings*. Subcostal area with at least weakly expressed pseudoveinlets. FW anal area hind margin at least somewhat weakly concave, anal angle at least weakly developed into a process, obtuse to narrowly triangular and tooth-like, a single cell row distad of Cup + 1a, this often divided by oblique crossveins and thus appearing as two distinct but irregular rows. HW anal area with three complete rows of cells. *Abdomen*. Tergum with posterior margin of each tergite diffusely darkened. *Males*. GPC not everted. Parameres unproduced. *Females*. Interdens present.

Synapomorphies.—antennal flagellum robust, nodes broadly pale; FW subcostal area undulations pigmented, forming distinct pseudoveinlets; segments 7 and 8 of male not hood-like.

Discussion.—*Haploglenius abdominevittatus* is the most derived member of this group, but it shares features with *reticulatus* (e.g., cervical sclerite yellow, wide costal cells, etc.), which in turn expresses similarities with *aquilonius* (e.g., antennae robust; FW anal cell row divided by oblique crossveins, pale pterostigmata, etc.). These three species are only known from a few specimens, but from this limited number of records it appears they occur somewhat proximate to one another relative to other haplogleniine species (within a span of fewer than 2000 kilometers) in the northern latitudes of South America.

Haploglenius reticulatus *Navás 1923*

(A3 Figs. 43–44, 87)

Haploglenius reticulatus Navás, 1923

—Navás 1923b.11.16 r#737: 15, fig. I {OD: ♀, D. TS: not indicated [holotype by monotypy]. TL: Peru. TR: MNHN. Type specimen examined (see "Type material examined" below).}

—Penny 1978.09.15 r#5098: 13 {GD, L}

—Ábrahám 2013.04.30 r#?????: 185 {DIS, TL, TR, TS}

Notes: Ábrahám says type material lost, but specimen in loan material borrowed from MNHN.

Haploglenius luteus aberr. *latoreticulatus* van der Weele, 1909

—van der Weele 1909.01.05 r#420: 49 {not available: Arts. 45.5 (not available if infrasubspecific), 45.6.2 (infrasubspecific if used "aberration", "ab.", etc.), 45.6.4: (subspecific if author used "var.", "unless its author also expressly gave it infrasubspecific rank"}

—Ábrahám 2013.04.30 r#?????: 176 {DIS, TSP (of "*Haploglenius latoreticulatus* van der Weele" [=*Haplogleniuslatoreticulatus* Ábrahám), SYN, TL, TR, TS}

Haploglenius latoreticulatus van der Weele, 1909

—Ábrahám 2013.04.30 r#?????: 176 {D, DIS, RD: ♂♀, SYN}

—Onore et al. 2014.03.30 r#15564: 87–91, figs. 1-5 {misidentification of *Haploglenius neoguineensis* Navás: BIO, DIS, MOR}

Haploglenius latoreticulatus Ábrahám, 2013

—Ábrahám 2013.04.30 r#?????: 176 {Art 45.5.1: infrasubspecific name cannot be made available except by Commission; 'subsequent author's attempt to make infrasubspecific name available results in that author establishing a new name with its own authorship and date'}

Etymology and nomenclatural notes.—*reticulatus*: reticulatus (Latin), 'net-like'. Apparently in reference to the appearance of the wing veins in the anal area of the forewing.

Diagnosis.—Antennae long, reaching nearly to FW pterostigma, and robust, nodes swollen; antennomeres pale, diffusely darkening distally where they expand, clubs asymmetrically fusiform. Pleuron variegated, pleural stripes irregular and not well formed. Wings largely lacking pigment, though sometimes appearing slightly smoky overall, and apices faintly tinged. Wing venation more open than in other species. Costal cells mostly slightly wider than high. Subcostal veinlets diffusely margined. Subcostal area undulations maculated to form pseudoveinlets. FW anal angle somewhat produced, hind margin distad of it concave. FW anal area cell row with many oblique crossveins (undivided in one female). Wing apices slightlyfalcate. Male: pronotal valve and mesonotal acrotergite not developed.

Autapomorphies.—small to medium sized pleuritocavae present on segment 7.

Distribution.—Ecuador, Peru.

Description.—

Size (mm). Male: length of body 37, abdomen 27, forewing 44–48, hind wing 39–44, antennae 31. Female: length of body 33, abdomen 22, forewing 51, hind wing 45, antennae 31.

Head. Occiput base color dark reddish brown, an elongate diffuse yellow macula positioned laterally along margin of postorbital sclerite, and a smaller similar macula positioned dorsad of the first. Vertex dark sandy brown; setae often slightly denser on anterior surface, only moderately dense overall, moderately long, slender, slightly wavy, golden, with some dark brown setae mixed in anteriorly. Extra-torular sclerites medium to dark reddish brown. Paraocular band dusky dark orangish or reddish brown near antennae and laterad of frons, becoming yellow near margin of frons and clypeus, in female thinly orangish along orbital sclerite. Frons dusky dark orange, a diffuse dark brown sagittal line present in dorsal half; setae moderately dense, long, slender, dark brown. Clypeus yellow or orangish, laterally with somewhat dark but diffuse and irregular reddish brown maculations. Labrum concolorous with mesal portion of clypeus. Mandibles dull yellow basally, apices dark reddish brown. Labium pale yellow, thin dark brown sagittal line weakly expressed or absent in available specimens. Eyes large, very slightly dorsoventrally oblong, very slightly larger in ventral half. Antennae flagellomeres distinctly swollen at nodes, flagellum reddish brown, internodes subapically darker, nodes thinly pale, verticils absent; clubs elongate, asymmetrical and somewhat fusiform, apices distinctly acuminate, in female completely yellow, in male posteriorly dull pale brown, anteriorly yellow, covered in fine pale setae.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite predominately yellow, dorsally dark brown. *Pronotum.* Anterior flange somewhat narrow, slightly produced dorsad. Posterior flange of female barely covering mesoacrotergite, in males slightly more produced but not valve-like, ventral surface not visible, presence of white crystalline material presumed absent. Pronotum base color dark brown, anterior flange anterolaterally paler, medial transverse band with some small, irregular maculations, sometimes sublaterally paler, posterior flange evenly brown, posterolateral margin narrowly yellow. All surfaces with long, very fine, brown setae. *Pteronotum*. Evenly dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum yellow and occasionally mesal and lateral areas of posterior swelling of mesoscutellum with very faint diffuse yellow maculations; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter, but stripes embedded with brown maculations, giving pleuron a somewhat variegated appearance; pleural setae somewhat dense, moderately long, slender, pale yellow, stripes occasionally with a light dusting of pruinescence.

Legs. Femora and tibiae base color orangish yellow, pro- and mesothoracic femora mesally to completely dark dusky brown, anterolateral faces of tibiae also dusky dark brown, distal third of femur and proximal third of tibia on anterolateral surfaces of metathoracic leg often slightly darker; tarsi dark reddish brown to almost black, terminal tarsomere pale reddish or orange in distal one-fourth. Coxae setae very pale yellow to white; antennal comb setae copper colored.

Wings. Dimension and shape. Long, moderately narrow, apex posteriorly subacute, posterior margins very slightly falcate. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, cells wide, cell height two-thirds to one-half of cell width in proximal half, width becoming narrower than height near pterostigma. Pterostigma with four to five forked and unforked pale yellow veinlets; membrane pale yellow, translucent, distal margin of pigment slightly produced one cell width along Sc+R, and Sc+R pale brown to yellow a short distance distad of pterostigma. Deltus brown, anteromesally darkening and becoming slightly opaque. Presectoral area with ca. eleven to twelve cells. Rs with six forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine to ten irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin somewhat weakly concave in males, more strongly concave in female, anal angle weakly developed into a process and not yet tooth-like, more developed in female, in female a single cell row distad of Cup + 1a and cells undivided by crossveins, in males cell row distinctly divided by oblique crossveins and thus appearing as two distince but irregular rows. *Color and patterning.* Venation dark brown. Costal and subcostal areas at least weakly fuscous, at least in female, subcostal veinlets diffusely margined; subcostal area with at least weakly expressed pseudoveinlets. Apex of wing often weakly fuscous, darkest in anterior portion of apical area. Entire wing membrane at least very slightly tinged with brown. HW. As in FW except as follows. Mp_2 fork angle approximately 90°. Medial triangle distal domain with two cells. Pre-Cup axillary disk yellow. Pre-Mp_1 area margin unexpanded or expansion very slight and broad. Anal area with three complete rows of cells. *Color and patterning.* Subcostal area with pseudoveinlets sometimes reduced to anterior spots.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly brown, posterior margin of each tergite diffusely darkened; T1 and T2 with moderately dense, long, wispy, golden brown setae, remainder of tergum devoid of long setae. *Sternum*. More or less medium to dark brown, S1 and S2 diffusely yellowish laterally; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, devoid of long setae.

Male terminalia. Unmacerated specimens. Somewhat small pleuritocavae visible at posterior margin of pleural membrane of segment 7, wrinkled, reddish brown, GPC not everted, pulvini not visible, ectoprocts and S9 dark reddish brown. *Macerated specimens.* Pleuritocavae somewhat small, a few times longer than width at base, surface convoluted with a dense coat of microsetae, length of pleuritocava of segment 8 very short, one-third to one-half that of segment 7. S9 apical margin obtusely angled, but very weakly, nearly straight. Pulvini somewhat small, very weakly sclerotized, length about coequal to width at base, bearing several very long, somewhat slender, brown setae. GPC somewhat weakly sclerotized; in lateral view dorsal margin somewhat raised in basal half, mesally weakly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view rather broad basally, converging apicad, with a weakly undulating lateral margin. Parameres in ventral view with anterolateral margin weakly angulate, proximolateral margins somewhat weakly differentiated. Pelta sclerotized, narrowly almond shaped.

Female terminalia. Unmacerated specimens. Unavailable. *Macerated specimens.* Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. two times width. Linguella only weakly differentiated from surrounding membrane, unsclerotized, bearing several short, stiff, slender, setae. Interdental space small, more or less round. Interdens sclerotized, short, cone-shaped.

Variation. The type specimen (JRJ_01218) with wings strongly tinged with brown, submelanistic. The female matches the male in nearly all aspects, but differs in the constitution of cells in the anal cell row and in the wings being narrower at their bases.

Type material examined.—*Holotype*, female, Peru, in MNHN collection: "MUSEUM PARIS Perou Rene Martin 1920 /// Peroú /// TYPE /// Haploglenius reticulatus Nav. Navas S.J. det. /// LECTOTYPE /// Haploglenius reticulatus Navás, 1923 Lectotype J. Legrand det. 1991 /// JRJ_01218". Condition: poor, mostly destroyed, antennae and wings spread, thorax and head crushed and glued back together, right antennae, all legs except one, left FW tip, and abdomen missing, all wings torned or with dings.

Additional material examined.—*Ecuador*: Morona-Santiago (BMNH: 1 ♂, JRJ_01639; MFNB: 1 ♀, JRJ_00640 [A3 Fig. 44]); Sucumbios (FSCA: 1 ♂, JRJ_00621 [A3 Fig. 43]).

Morphology, biology and ecology.—As explained under 'Discussion' below, this species bears a strong but superficial resemblance to *neoguineensis*, and their geographic ranges are somewhat proximate to one another (< ca. 150 km), at least within Ecuador (see A3 Figs. 87, 95). From the limited number of specimens and records available, however, they do not appear to be sympatric; rather, their ranges seem to be sharply divided by the Andes.

Discussion.—The labels of the holotype of *reticulatus* match those recorded by Navás in his original description, and there is no evidence to suggest Navás described the species from more than a single specimen (rendering unnecessary the recent 'lectotype' designation indicated by LeGrand's label). The holotype is in extremely poor condition but matches well two other specimens available in loan material, which include a male and a female, and which were very useful in redescribing the species. The poor condition of the type make it rather difficult to determine its sex, but based on the shape of the HW it appears to be a female. This agrees with the designation of Navás in his description.

Despite a superficial resemblance in the overall lack of wing pigment, a reduction in number of costal veinlets, the presence of pseudoveinlets, and a slight falcation in the wing apices, *reticulatus* is not conspecific with *neoguineensis*, as proposed by Ábrahám (2013, as "*latoreticulatus*") and followed by Onore et al. (2014). In *neoguineensis* the male has a well-developed pronotal valve and a well-developed, bilobed acrotergite like that of *luteus* and *brunneus*; in *reticulatus*, the valve is undeveloped and the acrotergite is not bilobed. These two species also differ in the shape of the FW anal margin, and in the expression of the oblique crossveins in the FW anal cell row; in *reticulatus* the anal margin is more prominent and the margin distad of the process is more concave, and the crossveins are more are numerous, often dividing every cell (the female of JRJ_00640 [A3 Fig. 44] is exceptional in having no crossveins), and begin proximally, as opposed to distally as in other species; in *neoguineensis* the anal angle is not as prominent, the margin distad of it not nearly as concave, and only a few of the distal cells of the anal area cell row are divided.

Haploglenius aquilonius *new species*

(A3 Figs. 45, 87)

Etymology and nomenclatural notes.—*aquilonius*: aquilonius (Latin), 'northern, northerly'. Named for the type locality of the holotype from the northernmost part of South America (northern Venezuela).

Diagnosis.—Antennae long, reaching nearly to FW pterostigma, and robust, nodes swollen, antennomeres pale with nodes diffuselydarkened. Pleural stripes imbedded with brown maculations, giving pleuron a variegated appearance. Wings with costal and subcostal areas tinged with pale brown color. Apical areas faintly tinged near pterostigmata. Costal cells' width coequal to or narrower than height. Subcostal area undulations weakly maculated to form diffuse pseudoveinlets. FW anal angle somewhat produced, hind margin distad of it concave. FW anal area cell row with many oblique crossveins. Male: pronotal valve not developed. Female: Unknown.

Autapomorphies.—FW anal angle somewhat well-developed but lateral margins of process still obtuse, posterior margin immediately distad of angle at least slightly concave.

Distribution.—North coastal Venezuela.

Description.—

Size (mm). Male: length of body 40, abdomen 28, forewing 50, hind wing 45, antennae 36.

Head. Occiput base color dark reddish brown, an elongate diffuse yellow macula positioned laterally along margin of postorbital sclerite, yellow posteroventrad of vertex and posterosagittal plate down to cervical membrane. Vertex dark sandy brown; setae moderately dense, moderately long, slightly wavy, dark golden brown setae. Extra-torular sclerites concolorous with frons, transversely narrowly dark brown. Paraocular band dusky medium to dark brown, slightly paler near margin of frons and clypeus. Frons dusky dark orange to moderately dark brown, a dark brown sagittal line present in dorsal half; setae moderately dense, long, slender, dark golden brown. Clypeus yellow, laterally diffusely dark brown. Labrum concolorous with mesal portion of clypeus. Mandibles dull yellow basally, apices dark reddish brown. Labium pale yellow. Eyes very slightly dorsoventrally oblong, very slightly larger in ventral half. Antennae flagellomeres distinctly swollen at nodes, flagellum pale brown, internodes subapically darker, nodes thinly pale, verticils absent; clubs elongate, asymmetrically fusiform, apices distinctly acuminate, pale yellow, posterior face narrowly and diffusely brown, covered in fine golden setae.

Thorax. Cervix. Dorsal cervical plate setae golden. Cervical sclerite dull dark brown. *Pronotum.* Anterior flange somewhat narrow, slightly produced dorsad. Posterior flange barely covering mesoacrotergite, not valve-like, ventral surface not visible, presence of white crystalline material on ventral surface presumed absent. Pronotum base color dark brown, anterior flange anterolaterally narrowly yellow, medial transverse band mesally and sublaterally with some small, irregular, diffuse, yellow maculations, posterior flange evenly brown, posterolateral margin narrowly yellow. All surfaces with long, very fine, dark golden brown setae. *Pteronotum*. Mesacrotergite not produced. Pteronotum proper evenly dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum yellow and mesal and lateral areas of posterior swelling of mesoscutellum with faint diffuse yellow maculations; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter, but stripes embedded with some brown maculations, giving pleuron a somewhat variegated appearance; pleural setae somewhat dense, moderately long, slender, pale yellow.

Legs. Femora and tibiae base color yellow, prothoracic femur posteriorly mesally dusky brown, pro- and mesothoracic femora dorsally and anterolaterally medium dusky brown, anterolateral faces of all tibiae dusky medium brown; tarsi medium reddish brown, terminal tarsomere pale orangish in distal one-third. Coxae setae very pale yellow to white; antennal comb setae golden.

Wings. Dimension and shape. Long, moderately slender, apex posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, width of cells more or less coequal to height, narrowing slightly in distal half of wing. Pterostigma with four to five forked and unforked pale yellow veinlets; membrane very pale yellow, translucent, distal margin of pigment straight. Deltus evenly brown, translucent. Presectoral area with ca. thirteen to fourteen cells. Rs with six forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. eleven to twelve irregular but more or less complete rows of cells. Cubital triangle distal domain with three cells. Anal area hind margin somewhat weakly concave, anal angle somewhat developed into a process but not yet tooth-like, cell row distad of Cup + 1a divided by oblique crossveins and thus appearing as two distinct but irregular rows. *Color and patterning.* Venation medium brown. Costal and subcostal areas weakly fuscous, with pigment narrowly absent along anterior margin of costal cells; subcostal area with at least weakly expressed pseudoveinlets. Apex of wing very weakly fuscous in anterior portion of apical area. HW. As in forewing except as follows. Mp_2 fork angle 90°. Medial triangle distal domain with two to three cells, but rather short. Pre-Cup axillary disk yellow. Pre-Mp_1 area margin expansion very slight and broad. Anal area with three complete rows of cells.

Abdomen. Not quite reaching to pterostigma with wings folded back. *Tergum*. Evenly brown, posterior margin of each tergite dorsomesally diffusely darkened; T1 and T2 with moderately dense, long, wispy, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. S1 and S2 laterally pale yellowish, mesally diffusely brown, with a dark brown sagittal line, S3 and S4 diffusely yellow, S5 to S8 medium to dark brown; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Brown, a pair of diffuse oblique yellow bands present; devoid of long setae.

Male terminalia. Unmacerated specimens. Pleuritocavae not visible, GPC not everted, pulvini not visible, ectoprocts and S9 dark reddish brown.

Macerated specimens. Not available.

Variation. Specimen JRJ_00620 is in rather poor condition. Although it is clearly allied to the type specimen, it may be teneral and has distinct differences in the coloration of the sclerites of the head, thorax, and legs. The face is almost entirely dull dark brown, including frons, paraocular band, clypeus, labrum, mandibles, and labium; patterns of thorax and legs muted.

Type material examined.—*Holotype* (A1 Fig. 00), **new designation**, male, Venezuela, in MFNB collection: “166 /// Puert. Cabell. Appus. /// costatus Burm. circumflexus et contrarius Walk. /// luteus N 19/3 /// Haloglenius luteus Walker /// HOLOTYPE Haploglenius aquilonius Jones ♂ design. J. R. Jones 2014 /// JRJ_01754”. Condition: excellent; antennae and wings spread, right FW tip missing, right HW tip torn, left pleuron with a hole (dermestids?).

Additional material examined.—*Venezuela*: Carabobo (FSCA: 1 ♂, JRJ_00620).

Morphology, biology and ecology.—The two known specimens of this species were collected at elevations of ca. 10 and 1200 m, the latter high in the Venzuelan Coastal Mountain Range, within Henri Pittier National Park.

Discussion.—This large and apparently rarely collected species is very similar to *luteus* in the shape of the wings, and to *reticulatus* in the robustness of the antennae and FW anal row crossveins. If differs from *luteus* in many ways, e.g. antennae robust and longer, pronotal valve in males undeveloped, FW anal row with numerous crossveins, etc.. It differs from *reticulatus* in being larger overall, in the antennae being longer, the wings being longer and narrower, the costals not being wide, the pseudoveinlets present but not well-developed, etc.

The sex of specimen JRJ_00620 is uncertain. The apex of the abdomen is missing, and as the holotype male has the pronotal valve unproduced, it is not possible to rely on that feature. The wings are folded over the back and quite tattered and so interpreting them is also problematic.

Haploglenius abdominevittatus *Ardila and Jones, 2012*

(A3 Figs. 46–47, 87)

Haploglenius abdominevittatus Ardila and Jones, 2012

—Ardila and Jones 2012.04.13 r#14570: 41 {OD: ♂, BIO, D, DIS, ET, FP, HAB, MOR. TS: holotype by original designation. TL: "Colombia (Orinoco), Vichada, Tuparro National Park". TR: MHN-ICN. Type specimen not examined (see "Discussion" below).}

—Ábrahám 2013.04.30 r#?????: 175 {GD, L, TL, TR, TS}

Etymology and nomenclatural notes.—*abdominevittatus*: abdomen (Latin), 'belly' + vittatus (Latin), 'banded, striped', = 'striped abdomen'. Named for broad pale bands encircling the anterior portions of the abdominal segments.

Diagnosis.—Antennae somewhat robust, nodes slightly swollen, antennomeres basally narrowly pale and distally dark, verticils present but not numerous. Thoracic pleuron with a variegated pattern. Costal area cells mesally slightly wider than high. FW anal angle well-developed into a triangular process, hind margin distad of it very concave. Anal area cell row narrow, undivided by oblique crossveins. HW basally narrowed, but anal area with three cells rows. Wings largely lacking pigment, but subcostal area undulations. Female: HW apex with a diffuse-margined round brown macula. maculated to form spots or pseudoveinlets; Sc yellow between subcostal veinlets; pterostigma veinlets dark brown. Anterior third of basal tergites slightly pale, forming a broad banding pattern. Male: pronotal valve developed.

Autapomorphies.—clypeus dorsolaterally with vague diffuse darkening or very small incipient or vestigial maculations; male pronotum posterodorsal margin produced into an articulable flap or valve, interior surface with white coating; male pronotal valve with wrinkles; pleuron variegated, with equal parts yellow and brown and no stripe; basal 4 tarsomeres reddish brown, terminal tarsomere yellow; FW anal angle very well developed and produced, lateral margins acute and process triangular, posteror margin immediately distad of angle distinctly concave; radius distinctly banded brown and yellow; FW anal area with a single row of cells roughly parallel to Cua, not split by crossveins; male HW distal domain absent.

Distribution.—Colombia, Venzuela.

Description.—

Size (mm). Male: length of body 36, abdomen 26, forewing 43, hind wing 36, antennae 31. Female: length of body 29, abdomen 21, forewing 44, hind wing 40, antennae 30.

Head. Occiput not visible. Vertex dark sandy brown; setae denser on anterior surface, only moderately dense overall, long, slender, slightly wavy, anteriorly white with some dark brown setae mixed in, dorsally and posteriorly mixed dark brown and white. Extra-torular sclerites concolorous with frons. Paraocular band dark brown, diffusely paler along orbital sclerite. Frons dusky medium dark brown, a diffuse dark brown medial macula present; setae moderately dense, long, slender, white, dorsolaterally dark brown. Clypeus very pale yellow, laterally with somewhat dark but diffuse and irregular reddish brown maculations. Labrum concolorous with mesal portion of clypeus. Mandibles dull pale yellow basally, dark reddish brown in distal half. Labium pale yellow, a thin dark brown sagittal line weakly expressed. Eyes nearly symmetrical. Antennae flagellomeres distinctly swollen at nodes, flagellum dark brown, nodes very pale, verticils present but not numerous; clubs elongate pyriform, apices weakly acute, predominately dark brown, ventral face diffusely pale yellow, distribution of pigment somewhat irregular in female, covered in fine dark brown setae.

Thorax. Cervix. Dorsal cervical plate not visible. Cervical sclerite dark brown with apical surface yellow. *Pronotum.* Anterior flange somewhat narrow, slightly produced dorsad. Posterior flange of female barely covering mesacrotergite, in male valve-like, overlapping acrotergite nearly to midpoint of anterior swelling of mesoprescutum, ventral surface with a dense coating of white crystalline material. Pronotum base color dark brown, anterior flange anterolaterally paler, medial transverse band with some small, irregular maculations mesally, sublaterally and on posterior face of posterolateral knob, posterior flange evenly brown, posterolateral margin narrowly pale yellow. All surfaces with long, very fine, brown setae. *Pteronotum*. Mesacrotergite not produced. Pteronotum proper more or less evenly dark earthy brown, diffusely pale yellow on lateral surface of mesoprescutum and on tegular area of mesoscutum, very faint diffuse pale brown maculations present on lateral area of posterior swelling of mesoscutellum; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, long, slender, mixed dark and pale golden brown setae. *Pleuron* base color dark brown, oblique yellow stripes poorly formed, incomplete, and largely interrupted by embedded brown maculations, pleuron having a variegated appearance; pleural setae somewhat dense, long, slender, mixed dark brown and pale yellow.

Legs. Femora and tibiae base color pale yellow, distal third of anterolateral surface of femora and proximal third of anterolateral surface of tibiae dusky dark brown; tarsi first four tarsomeres pale reddish brown, distal tarsomere amber yellow. Coxae setae very pale yellow to white; antennal comb setae copper colored.

Wings. Dimension and shape. Long, moderately narrow, bases narrowed, apices rounded. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, cells wide, cell height two-thirds to one-half of cell width in proximal half, width becoming narrower than height near pterostigma. Pterostigma with four to five forked and unforked dark brown veinlets; membrane dusky brown, translucent, distal margin straight. Deltus colorless to very slightly tinged with brown pigment, translucent. Presectoral area with ca. nine to ten cells. Rs with five forks. Mp_2 + Cua_1 sharply curving toward hind margin in distal portion. Cubital area with ca. nine to eleven irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin strongly concave, anal angle well developed into a triangular, tooth-like, process, a single narrow cell row distad of Cup + 1a with cells undivided by crossveins. *Color and patterning.* Venation dark brown, Sc yellow between subcostal veinlets. Costal and subcostal areas devoid of fuscous pigment, subcostal area with pseudoveinlets. In male, apex of wing very weakly fuscous, female lacking pigment. HW. As in forewing except as follows. Mp_2 fork angle approximately 90°. Medial triangle distal domain essentially absent. Pre-Cup axillary disk pale yellow, proximally flecked with dark brown pigment. Pre-Mp_1 area margin unexpanded, hind margin weakly invaginated at Mp_{2p}. Anal area with three complete rows of cells. *Color and patterning.* Subcostal area with pseudoveinlets sometimes reduced to anterior spots. In female, HW apex with a large fuscous maculation.

Abdomen. In male not quite reaching to pterostigma with wings folded back; in female, not reaching to pterostigma, much shorter. *Tergum*. Base color dark brown, T1 and T2 dark brown, proximal half of T3 and T4 with texture of golden microsetae giving tergites a very pale appearance, T5 to T8 also with pale microsetae; abdomen overall with a light-dark banding pattern; T1 and T2 with moderately dense, long, wispy, mixed pale yellow and dark brown setae, remainder of tergum devoid of long setae. *Sternum*. Base color brown to dark brown, with irregular, diffuse areas of pale brown coloration; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown with some irregular pale brown to yellowish mottling; devoid of long setae.

Male terminalia. Unmacerated specimens. Pleuritocavae very short on posterior margin of pleural membrane of segment 7, GPC not everted, pulvini not visible, ectoprocts and S9 dark reddish brown, apex of ectoprocts narrowly pale.

Macerated specimens. Pleuritocavae very short, pouch-like. S9 apical margin obtusely angled, nearly acute. Pulvini somewhat small, very weakly sclerotized, length slightly longer than width at base, bearing several very long, slender, brown setae subapically, and a very long slender seta apically. GPC somewhat sclerotized; in lateral view dorsal margin somewhat raised in basal half, mesally distinctly notched, ventrally more or less entire, dorsal and ventral margins convergent; in ventral view somewhat broad basally, lateral margins slightly undulating and converging apicad. Parameres in ventral view with proximal margins weakly differentiated. Pelta weakly sclerotized, almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae and distivalvae pale brownish yellow, ectroprocts brown with apical margins pale brownish yellow.

Macerated specimens. Not available.

Variation. Too few specimens available to make any determinations about variations.

Type material examined.—Holotype specimen discussed in detail with co-author A. Ardila Camacho (Ardila and Jones, 2012), but not borrowed for this study.

Additional material examined.—*Venezuela*: Amazonas (USNM: 1 ♂, JRJ_00597 [A3 Fig. 46], 1 ♀, JRJ_00596 [A3 Fig. 47]).

Morphology, biology and ecology.—The Venezuela specimens were collected in a malaise trap placed over a dry stream channel at 760 m.

Discussion.—This species is unique among NWH in completely lacking fuscation in the costal and subcostal areas, and in having a well-developed anal angle *and* three complete rows of cells in the anal area of the HW. Its abdominal banding pattern is very subtle and somewhat difficult to see, and seems to be formed from the reflection of light off of pale microsetae. Like members of the *appendiculatus* species group, the dorsum expresses mixed dark (nearly black) and pale grayish setae, the pleural stripes are poorly developed, and the antennae have a few verticils. But these similarities appear to represent convergences. The loss of the pleural stripe in *abdominevittatus* is similar to that seen in the closely related species *reticulatus* and *aquilonius*, and the verticils are very sparse and quite different from those in the *appendiculatus* species group.

flavicornis *species group*

Diagnosis.—*Head*. Vertex setae moderately dense, mixed dark brown and golden yellow. Antennae with color variable, often yellow, with nodes paler; clubs fusiform, apices distinctly acuminate. *Thorax*. In males, pronotum posterior flange not developed into an articulating valve. Pleuron with a pair of oblique pale stripes. *Legs*. Tarsi medium to dark reddish-brown, proximal margins dark brown and tarsi appearing annulated. *Wings*. Narrowed at bases, apices posteriorly subacute. Costal areas usually fuscous, at least in FW. FW anal angle well developed, triangular and tooth-like, anal area hind margin distinctly concave, a single narrow cell row distad of Cup + 1a. HW anal area with two complete rows of cells. *Abdomen*. Posterior margin of each tergite narrowly and diffusely darkened. Pleural membrane dark brown, sometimes with ca. four to five oblique yellow bands, these usually more vivid in females. *Males*. Pleuritocavae visible at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, a second pair sometimes visible at posterior margin of segment 8 but very short. T7 posteromesal margin distinctly hood-like, T8 usually completely pale yellow, rarely posteromesal surface with a black maculation, T9 dorsally pale yellow. GPC sometimes slightly everted. Parameres unproduced. *Females*. Interdens present.

Synapomorphies.—cervical sclerite apex yellow, other surfaces brown; HW costal area unexpanded, C parallel to Sc along entire length; HW anal area with two rows of cells roughly parallel to Cua; FW pterostigma with first veinlet commencing at Sc-R anastomosis but distinctly and consistently oblique to Sc, last nearly in line with R.

Discussion.—Penny (1982a) placed *flavicornis* and *angulatus* in his new genus *Neohaploglenius*. He later (2002) synonymized them, but morphological and molecular (unpublished) data indicate they are separate. Cladistic analysis placed them together with high support (A3 Fig. 1 node 33).

Haploglenius flavicornis *McLachlan 1871*

(A3 Figs. 48, 88)

Haploglenius flavicornis McLachlan, 1871

—McLachlan 1871.09.14 r#353: 235 {OD: ♀, D, DIS. TS: not indicated [holotype—see van der Weele 1909]. TL: “Cuernavaca, Mexico”. TR: “collection of Baron de Selys Longchamps” (SELYS—see Oswald 2013a). Type specimen not examined (see “Discussion” below).}

—Gerstaecker 1894 r#2559: 94 {DIS, MOR}

—van der Weele 1906 r#404: 226 {DIS}

—van der Weele 1909.01.05 r#420: 52, fig. 26 {D, DIS, GD, MOR, RD: ♂♀, TL, TR, TS}

—Navás 1929.02.?? r#860: 109 {D, GD, L}

—Shetlar 1977 r#5727: 93, figs. 24a–d, 39 {Ph.D. dissertation, nomenclatural acts invalid: D, DIS, GD, MOR, RD: ♂♀, SR, SYN, TL, TR, TS}

—Penny 1978.09.15 r#5098: 13 {GD, L, SYN}

—Penny 1982a r#5105: 398 {TSP (of *Neohaploglenius* new genus)}

—Penny 1982b r#5103: 626 {DIS, TSP (of *Neohaploglenius* new genus)}

—Oswald and Penny 1991.12.02 r#7138: 42 {TSP (of *Neohaploglenius* new genus)}

—Penny 2002.10.21 r#10230: 179 {DIS, SYN}

—Ábrahám 2013.04.30 r#?????: 175, 179 {GD, SYN}

Neohaploglenius flavicornis (McLachlan, 1871)

—Penny 1982a r#5105: 401 {GD, NC}

—Penny 2002.10.21 r#10230: 180, figs. 2, 11 {AD, D, DIS, GD, FP, HAB, MOR, SYN}

—Ábrahám 2013.04.30 r#?????: 175, 179 {NS, SYN}

Haploglenius dentiger Gerstaecker, 1894

—Gerstaecker 1894 r#2559: 94 {OD: ♀, D, DIS. TS: not indicated [holotype by monotypy—see also van der Weele 1909]. TL: "Chiriqui" (Panama). TR: not indicated (EMAU—see van der Weele 1909 fig. 26 caption, Oswald 2013a). Type specimen not examined (see "Discussion" below).}

—van der Weele 1906 r#404: 226 {DIS, TS}

—van der Weele 1909.01.05 r#420: 52 {JSYN (of *Haploglenius flavicornis* McLachlan), MOR}

—Shetlar 1977 r#5727: 93 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Haploglenius flavicornis* McLachlan)}

—Penny 1978.09.15 r#5098: 13 {JSYN (of *Haploglenius flavicornis* McLachlan)}

—Ábrahám 2013.04.30 r#?????: 175, 179 {JSYN (of *Haploglenius flavicornis* McLachlan)}

Etymology and nomenclatural notes.—*flavicornis*: flavus (Latin), 'yellow' + cornu (Latin), 'horn', = 'yellow horn'. Refers to the yellow antennae.

Diagnosis.—HW strongly narrowed at base, nearly as much as FW. Deltus consistently dark brown and opaque anteromesally, narrowly translucent posteriorly. HW medial triangle distal domain unproduced or with a single short cell; anal are with cells in both rows subtending Cua very small, coequal in height with cells in medial triangle, and similar in height, width, and shape to each other. Pleuritocavae large, corkscrewing.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Costa Rica, Guatemala, Mexico, Panama.

Description.—

Size (mm). Male: length of body 31–36, abdomen 23–26, forewing 39–46, hind wing 35–41, antennae 26–32. Female: length of body 32–33, abdomen 23, forewing 46–51, hind wing 43–45, antennae 27–30.

Head. Occiput with pattern variable and irregular, reddish brown near cervical membrane and ventrally, laterally and immediately dorsad of cervical membrane with large diffuse blotches of yellow. Vertex medium to dark sandy brown; setae moderately dense, long, slender, mixed dark brown and golden yellow. Extra-torular sclerites concolorous with frons. Paraocular band dark brown near antennae, dusky brown to somewhat yellowish laterad of frons, narrowly pale yellow near margin of frons and clypeus, narrowly pale orangish or yellowish along orbital sclerite. Frons dusky medium to dark orange, often with a reddish-brown sagittal maculation; setae moderately dense, long, slender, golden yellow with some dark brown mixed laterally and dorsally. Clypeus yellow, often laterally diffusely tinged with reddish-brown. Labrum concolorous with mesal portion of clypeus. Mandibles pale or dull yellow basally, becoming dark reddish-brown distally. Labium pale amber yellow, distal margin sublaterally sometimes slightly darkened. Eyes very slightly dorsoventrally oblong. Antennae flagellomeres slightly swollen at nodes, antennae coloration somewhat variable, flagellum pale yellowish- or reddish-brown to dark reddish-brown, nodes paler, verticils absent; clubs fusiform, apices often distinctly acuminate, sometimes very slightly rounded apically, base color yellow, often anterior face diffusely and longitudinally reddish to dark brown, opposite face sometimes slightly darkened, covered in fine golden setae.

Thorax. Cervix. Dorsal cervical plate setae golden yellow. Cervical sclerite apex dull yellow, subapical surface to base medium to dark brown. *Pronotum.* Anterior flange narrow, somewhat produced dorsad. Posterior flange of females just barely covering mesoacrotergite; males nearly identical to females, except slightly more produced, barely covering mesacrotergite, white crystalline material absent. Pronotum coloration evenly medium to dark brown, posterior margin of posterior flange sublaterally narrowly yellow. All surfaces with moderately long, very fine, golden brown setae. *Pteronotum*. Evenly dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum yellow and occasionally mesal and lateral areas of posterior swelling of mesoscutellum with very faint diffuse pale brown to yellow maculations; velvety spots of metascutum dark reddish-brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae more or less even, somewhat dense, moderately long, slender, mixed golden yellow and white, stripes with pruinescence.

Legs. Femora of pro- and mesothoracic legs diffusely dusky dark brown on ventral and anterolateral surfaces, on prothoracic legs dusky brown in mesal third of dorsal and posterolateral surfaces; tibiae of pro- and mesothoracic and sometimes metathoracic legs pale to dark dusky brown on anterolateral surfaces, all other surfaces pale yellow to orange; tarsi medium to dark reddish-brown, proximal margins dark brown and tarsi appearing annulated, terminal tarsomere pale reddish or orange in distal two-fifths. Coxae setae very pale yellow to white; antennal comb setae golden.

Wings. Dimension and shape. Long, slender, especially HW, wings slightly more slender in males, FW strongly narrowed at base, HW also strongly narrowed nearly as much as FW, apex posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, width of cells more or less coequal to height in proximal half, width narrowing to nearly half of height in distal third. Pterostigma with four to six forked and unforked pale yellow to brown veinlets; membrane pale yellow to medium orangish-brown, translucent to slightly opaque, distal margin of pigment straight. Deltus consistently dark brown and opaque anteromesally, narrowly translucent distally. Presectoral area with ca. eleven to thirteen cells. Rs with ca. six to seven forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. eleven to thirteen irregular to more or less complete rows of cells. Cubital triangle distal domain with two to three cells distad of fork. Anal area hind margin distinctly concave, anal angle well developed, triangular and tooth-like, slightly longer than in *angulatus*, a single narrow cell row distad of Cup + 1a. *Color and patterning.* Venation pale to dark brown. Costal and subcostal areas fuscous, sometimes weakly, sometimes with pigment narrowly absent along anterior margin of basal costal cells, subcostal veinlets sometimes diffusely margined. Pre-sectoral area with anterior portions of cells diffusely fuscous. Apical area sometimes lightly fuscous along wing margin. Some specimens, both males and females, with entire wing membrane weakly tinged with brown, some males distinctly melanistic. HW. As in forewing except as follows. Mp_2 fork angle approximately 90°. Medial triangle distal domain unproduced or with a single short cell. Pre-Cup axillary disk pale to intensely yellow. Pre-Mp_1 area margin greatly reduced, straight to slightly concave proximad of Mp_{2p}. Anal area with two complete rows of cells, height of cells coequal to or narrower than width. *Color and patterning.* Costal area sometimes partially or completely lacking pigment, especially toward wing base, even in specimens where the FW costal area is completely fuscous.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Medium to dark earthy brown, occasionally posterior margin of each tergite narrowly and diffusely darkened; T1 and T2 with intermediately dense, moderately long, wispy, golden setae, remainder of tergum devoid of long setae. *Sternum*. Color variable, S1 to S2 sometimes yellow to orange with a thin sagittal brown line, sometimes becoming evenly dark brown, S3 to S4 often with diffuse irregular blotches of yellow, remaining sternites brown to dark brown, sometimes diffusely yellowish; mostly devoid of long setae, some intermediately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, sometimes with ca. four to five oblique yellow bands, these usually more vivid in females; devoid of long setae.

Male terminalia. Unmacerated specimens. Large, corkscrewing, pleuritocavae visible at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, a second pair sometimes visible at posterior margin of segment 8 but very short, T7 posteromesal margin distinctly hood-like, T8 usually completely pale yellow or dull brown, rarely posteromesal surface with a black maculation, T9 dorsally pale yellow, GPC sometimes slightly everted, pulvini not visible, ectoprocts dark brown, yellow dorsally and laterally, S9 dark brown. *Macerated specimens.* Pleuritocavae long, corkscrewing, length ca. three to four times width at base, surface convoluted with a dense coat of microsetae on anterior surface, length of pleuritocava of segment 8 somewhat small, a few times longer than width at base. S9 apical margin obtusely angled. Pulvini somewhat small, very weakly sclerotized, length about coequal to width at base, bearing many medium long, slender, brown setae. GPC somewhat sclerotized; in lateral view dorsal margin weakly arched in basal half, mesally notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view somewhat broad basally, lateral margins evenly and convergent apicad, or slightly undulating. Parameres in ventral view slightly short and broad, apically somewhat blunt, proximolateral margins somewhat well differentiated. Pelta sclerotized, almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae dull reddish to dark brown, distivalvae orangish-brown, ectroprocts orangish to dark brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views somewhat elongate, length ca. two times width, with setae moderately long and rather robust. Linguella undifferentiated from surrounding membrane, unsclerotized, bearing several short, very slender, very pale setae. Interdental space small, more or less round. Interdens sclerotized, round at base, short, cone-shaped or nipple-like.

Variation. Specimen JR_01631 (A3 Fig. 48), a female from Guatemala, has the facial sclerites and legs almost entirely evenly medium dark brown, and the notum evenly dull pale brown, but these are likely artifacts of collection medium.

Type material examined.—Not available for this study.

Additional material examined.—*Costa Rica*: Alajuela (BYUC: 1 ♂, JRJ_00849); Puntarenas (DEBU: 1 ♂, JRJ_00856; EMEC: 2 ♂♂, JRJ_00850, JRJ_00863, JRJ_00864, 1 ♀, JRJ_00867; SDMC: 4 ♂♂, JRJ_00847, JRJ_00848, JRJ_00851, JRJ_00877, 1 ♀, JRJ_00865; UCDC: 1 ♂, JRJ_00862; USNM: 1 ♂, JRJ_00886); San Jose (EMUS: 1 ♂, JRJ_00843; FSCA: 1 ♂, JRJ_00857). *Guatemala*: Alta Verapaz (FSCA: 1 ♂, JRJ_00831, 1 ♀, JRJ_00833); Baja Verapaz (JRJC: 1 ♂, JRJ_10209); Huehuetenango (JRJC: 1 ♀, JRJ_10124). *Panama*: Chiriqui (INPA: 1 ♂, JRJ_00887; TAMU: 1 ♂, JRJ_00885).

Morphology, biology and ecology.—Some loan material specimens were taken at lights, including UV lights. Elevations recorded on labels ranged from approx. 1150 to 1700 m, and some locations entered into GoogleEarth are at elevations exceeding 2600 m, indicating that *flavicornis* may be exclusively a higher elevation species (localities for *angulatus* were at elevations ranged from 2100 m down to near sea level in coastal areas). Collection localities on labels for *flavicornis* were from Guatemala, Costa Rica and Panama, and the type is from Mexico; specimens probably also occur in El Salvador, Honduras and Nicaragua.

Specimen JRJ_00863, a male from Costa Rica, has ca. seven yellow, long-legged, mites of various sizes embedded in its thoracic pleural setae between the prothoracic coxa and the mesobasisternum on both sides of the thorax, and on the right prothoracic femur. It is not clear if these are phoretics or if they are feeding, but a few seem to have their mouthparts attached to the integument.

Discussion.—This species is very similar to and sympatric with *angulatus* Gerstaecker. The shape of the base of the wings is critical in differentiating the two species (see discussion for *angulatus*, below), but other diagnostic features are also useful, including the length of the medial triangle distal domain and the size of the pleuritocavae (see Diagnosis above). These latter features are different from those provided by van der Weele (1909) or discussed by Penny (2002). DNA sequence data (unpublished) also indicates substantial genetic distance between the two species.

Van der Weele (1909) interpreted Gerstaecker's *dentiger* to be conspecific with *flavicornis*. Gerstaecker (1894) described his species *dentiger* from Panama and differentiated it from *flavicornis* by having darkened wings and yellow pterostigmata. He also compared it to *angulatus*, but stated that the hind margin of the FW was more strongly cut at the base, causing the process to appear to protrude further. He further pointed out that posterad of Cua the wing and its cell rows are very narrow. All of this suggests that Gerstaecker's *dentiger* is a synonym of *flavicornis*.

Haploglenius angulatus *Gerstaecker, 1894 new status*

(A3 Figs. 49–50, 89)

Haploglenius angulatus Gerstaecker, 1894

—Gerstaecker 1894 r#2559: 93 {OD: ♂♀, D, DIS. TS: not indicated [syntypes, sex unknown; a lectotype needs to be designated from syntype material]. TL: "Chiriqui" (Panama). TR: not indicated (possibly EMAU—see TR for *Haploglenius dentiger* Gerstaecker, Oswald 2013a). Type specimen not examined (see "Discussion" below).}

—van der Weele 1906 r#404: 226 {DIS}

—van der Weele 1909.01.05 r#420: 51, fig. 25 {D, GD, RD: ♂♀, TS}

—Navás 1929.02.?? r#860: 109 {D, GD, L}

—Shetlar 1977 r#5727: 93 {Ph.D. dissertation, nomenclatural acts invalid: DIS, JSYN (of *Haploglenius flavicornis* McLachlan), MOR}

—Penny 1978.09.15 r#5098: 12 {GD, L}

—Penny 2002.10.21 r#10230: 179 {DIS, JSYN (of "*Neohaploglenius flavicornis* (McLachlan)" [=*Haploglenius flavicornis* McLachlan]), MOR}

—Ábrahám 2013.04.30 r#?????: 175, 179 {JSYN (of *Haploglenius flavicornis* McLachlan)}

Neohaploglenius angulatus (Gerstaecker, 1894)

—Penny 1982a r#5105: 401 {GD, L}

—Ábrahám 2013.04.30 r#?????: 175, 179 {JSYN (of *Haploglenius flavicornis* McLachlan)}

Etymology and nomenclatural notes.—*angulatus*: angulatus (Latin) 'cornered, angular'. In reference to the developed anal process of the forewing.

Diagnosis.—HW somewhat narrowed at base, but not nearly as much as FW. Deltus sometimes dark brown and opaque anteromesally, but often paler and translucent. HW medial triangle distal domain short, with one to two cells; anal are with cells in both rows subtending Cua taller than cells in medial triangle, posterior row with cells much taller than wide, a few cells sometimes divided by crossveins. Pleuritocavae medium-sized, sometimes corkscrewing slightly.

Autapomorphies.—basal cell of HW costal area anterodistally thickened and dark brown over a large area, almost completely covering membrane, otherwise mostly translucent to clear.

Distribution.—Brazil, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Venezuela.

Description.—

Size (mm). Male: length of body 30–39, abdomen 22–30, forewing 38–44, hind wing 34–40, antennae 26–28. Female: length of body 32–35, abdomen 22–25, forewing 47–56, hind wing 42–50, antennae 26–33.

Head. Occiput with pattern variable and irregular, reddish brown near cervical membrane, laterally with large diffuse blotches of yellow. Vertex medium to dark sandy brown; setae moderately dense, moderately long, slender, mixed dark brown and golden yellow. Extra-torular sclerites concolorous with prefrons. Paraocular band dark brown near antennae, dusky brown laterad of frons, narrowly yellow near margin of frons and clypeus, narrowly pale orangish or yellowish along orbital sclerite. Frons dusky medium to dark orange, often with a narrow, diffuse, usually incomplete reddish brown sagittal line; setae moderately dense, moderately long, slender, mixed golden yellow and dark brown. Clypeus yellow, occasionally laterally with diffuse reddish brown maculations. Labrum concolorous with clypeus. Mandibles pale yellow basally, dark reddish brown in distal half. Labium pale amber yellow, sometimes with a very thin diffuse red sagittal line present, often incomplete or absent. Eyes very slightly dorsoventrally oblong, very slightly larger in ventral half. Antennae flagellomeres slightly swollen at nodes, antennae coloration somewhat variable, flagellum pale yellow to dull or dark reddish brown, often completely and distinctly yellow, nodes paler, verticils absent; clubs fusiform, apices distinctly acuminate, yellow, sometimes with a very narrow longitudinal dark brown line, covered in fine golden brown setae.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite color variable, apex dull yellow, sometimes darkening to medium brown, subapical surface to base medium to dark brown. *Pronotum.* Anterior flange narrow, somewhat produced dorsad. Posterior flange of females just barely covering mesacrotergite, in males only very barely covering mesacrotergite, white crystalline material absent. Pronotum coloration evenly medium to dark brown. All surfaces with moderately long, very fine, brown setae. *Pteronotum*. Evenly dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum yellow and occasionally mesal and lateral areas of posterior swelling of mesoscutellum with very faint diffuse pale to orangish maculations; velvety spots of metascutum dark reddish brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, mixed pale yellow and white, stripes with pruinescence.

Legs. Femora of pro- and mesothoracic legs diffusely dusky dark brown on ventral and anterolateral surfaces, sometimes completely covering femora; tibiae of pro- and mesothoracic legs pale to dark dusky brown on anterolateral surfaces, distal third of femur and proximal third of tibia on anterolateral surfaces of metathoracic leg often slightly darker, this sometimes spreading to entire anterolateral surfaces, all other surfaces pale yellow to orange; tarsi medium to dark reddish brown, proximal margins dark brown and tarsi appearing annulated, terminal tarsomere pale reddish or orange in distal two-fifths. Coxae setae very pale yellow to white; antennal comb setae golden.

Wings. Dimension and shape. Long, slender, especially HW, wings slightly more slender in males, FW strongly narrowed at base, HW somewhat narrow, apex posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, width of cells more or less coequal to height in proximal half, width narrowing to nearly half of height in distal half. Pterostigma with four to six forked and unforked brown veinlets; membrane pale to somewhat dark brown, usually medium brown, only slightly darker than costal area, usually translucent but sometimes becoming slightly opaque, distal margin of pigment often continuing diffusely and narrowly along margin of wing in apical area a few to many cell widths. Deltus medium to dark brown, translucent to opaque, often slightly darker anteromesally. Presectoral area with ca. eleven to thirteen cells. Rs with ca. six to seven forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. eleven to thirteen irregular to more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin distinctly concave, anal angle well developed, triangular and tooth-like, a single narrow cell row distad of Cup + 1a. *Color and patterning.* Venation pale to dark brown. Costal and subcostal areas fuscous, sometimes weakly, sometimes with pigment narrowly absent along anterior margin of basal costal cells, subcostal veinlets sometimes diffusely margined, occasionally pigment altogether absent. Presectoral area with anterior portions of cells diffusely fuscous, this sometimes continuing into radial area. Apical area sometimes lightly fuscous. Some specimens, both males and females, with entire wing membrane weakly tinged with brown. HW. As in forewing except as follows. Mp_2 fork angle approximately 90°. Medial triangle distal domain very short with one to two cells. Pre-Cup axillary disk variable, completely yellow to nearly completely dark brown, often yellow in posterior portions and dark brown anteriorly. Pre-Mp_1 area margin unexpanded. Anal area with two complete rows of cells, occasionally one or two distal cells with lateral veinlets forking to hind margin or split by a transverse crossvein. *Color and patterning.* Costal area sometimes partially or completely lacking pigment, especially toward wing base, even in specimens where the FW costal area is completely fuscous.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Medium to dark earthy brown, sometimes posterior margin of each tergite narrowly and diffusely darkened; T1 and T2 with moderately dense, moderately long, wispy golden setae, remainder of tergum devoid of long setae. *Sternum*. Color variable, S1 to S2 sometimes yellow to orange with a thin sagittal brown line, sometimes becoming evenly dark brown, S3 to S4 often with diffuse irregular blotches of yellow, remaining sternites brown to dark brown, sometimes diffusely yellowish; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, sometimes with ca. four to five oblique yellow bands, these usually more vivid in females; devoid of long setae.

Male terminalia. Unmacerated specimens. Medium sized pleuritocavae visible at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, a second pair sometimes visible at posterior margin of segment 8 but very short, T7 posteromesal margin distinctly hood-like, T8 usually completely pale yellow, rarely posteromesal surface with a black maculation, T9 dorsally pale yellow, GPC sometimes slightly everted, pulvini not visible, ectoprocts dark brown, yellow dorsally and laterally, S9 dark brown. *Macerated specimens.* Pleuritocavae medium length, a few times longer than width at base, sometimes curving and corkscrew-like, surface convoluted with a dense coat of microsetae on anterior surface, length of pleuritocava of segment 8 rather small, a few times longer than width at base, slightly curving. S9 apical margin obtusely angled. Pulvini somewhat small, very weakly sclerotized, length about coequal to width at base, bearing many medium to long, slender, brown setae. GPC somewhat sclerotized; in lateral view dorsal margin somewhat raised in basal half, mesally distinctly notched, ventrally more or less entire, dorsal and ventral margins subparallel to convergent apicad; in ventral view somewhat broad basally, lateral margins slightly convergent in proximal two-thirds, then strongly convergent in distal third. Parameres in ventral view slightly short and broad, proximolateral margins somewhat well differentiated. Pelta sclerotized, narrowly almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae dull reddish to dark brown, distivalvae often yellow, sometimes becoming darker, ectroprocts reddish to dark brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views somewhat elongate, length ca. two times width, with setae moderately long and rather robust. Distivalvae setae also slightly longer and more robust, but not as long and robust as on ventrovalvae. Linguella undifferentiated from surrounding membrane, unsclerotized, bearing several short, very slender, very pale setae. Interdental space small, more or less round. Interdens sclerotized, round at base, short, cone-shaped.

Variation. Specimen JRJ_00828 with the right HW surface area greatly enlarged; a second major longitudinal vein emerges from the axillary sclerites immediately posterad of R (Ma?), forking at its base and subsequently forking several times to nearly double the surface area of the wing. This genetic deformation is absent in the left HW. The height of the cells in the anal area of the HW varies somewhat, but in general are taller than wide and not as distinctly narrow as in *flavicornis*.

Type material examined.—Not available for this study.

Additional material examined.—*Brazil*: Amazonas (SDMC: 1 ♂, JRJ_00891); Rondônia (FSCA: 1 ♀, JRJ_00896); locality uncertain (MHNG: 5 ♀♀, JRJ_00890, JRJ_00892, JRJ_00893, JRJ_00894, JRJ_00895). *Costa Rica*: Alajuela (CUAC: 1 ♂, JRJ_00858, 1 ♀, JRJ_00883; EMUS: 2 ♂♂, JRJ_00842, JRJ_00844, 3 ♀♀, JRJ_00866, JRJ_00872, JRJ_00875; FSCA: 1 ♀, JRJ_00884; JRJC: 1 ♂, JRJ_10252; UMSP: 1 ♂, JRJ_00882, 2 ♀♀, JRJ_00880, JRJ_00881); Cartago (JRJC: 1 ♀, JRJ_10208); Guanacaste (CAS: 2 ♂♂, JRJ_00845, JRJ_00854, 2 ♀♀, JRJ_00870, JRJ_00878; EMEC: 1 ♂, JRJ_00853; EMUS: 3 ♂♂, JRJ_00841, JRJ_00846, JRJ_00852, 3 ♀♀, JRJ_00868, JRJ_00869, JRJ_00873; UMSP: 1 ♂, JRJ_00859); Heredia (SDMC: 1 ♀, JRJ_00879 [A3 Fig. 50]; UMMZ: 1 ♂, JRJ_00861); Puntarenas (USNM: 1 ♂, JRJ_00860); San Jose (EMUS: 1

♂, JRJ_00855, 2 ♀♀, JRJ_00871, JRJ_00874; FSCA: 1 ♂, JRJ_00876; USNM: 1 ♂, JRJ_00840). *El Salvador*: Ahuachapan (TAMU: 1 ♀, JRJ_00838); La Libertad (FSCA: 1 ♂, JRJ_00836); Santa Ana (CAS: 1 ♂, JRJ_00837). *Guatemala*: Alta Verapaz (FSCA: 1 ♀, JRJ_00832); Chimaltenango (UMSP: 1 ♀, JRJ_00828); Retalhuleu (TAMU: 2 ♂♂, JRJ_00829, JRJ_00830); Suchitepequez (WSU: 1 ♂, JRJ_01289, 3 ♀♀, JRJ_01287, JRJ_01288, JRJ_01291); Zacapa (WSU: 1 ♀, JRJ_01290). *Honduras*: Francisco Morazan (FSCA: 1 ♂, JRJ_00835); Olancho (FSCA: 1 ♂, JRJ_00834). *Mexico*: Chiapas (CAS: 1 ♂, JRJ_00746; EMEC: 1 ♂, JRJ_00728, JRJ_00755, 1 ♀, JRJ_00822; FSCA: 1 ♀, JRJ_00818; SDMC: 2 ♀♀, JRJ_00790, JRJ_00791); Colima (TAMU: 1 ♂, JRJ_00734); Durango (SDMC: 2 ♀♀, JRJ_00783, JRJ_00788); Guanajuato (EMEC: 1 ♂, JRJ_00715); Guerrero (FSCA: 1 ♀, JRJ_00820; SDMC: 1 ♂, JRJ_00744); Jalisco (EMEC: 2 ♂♂, JRJ_00761, JRJ_00779, 3 ♀♀, JRJ_00789, JRJ_00798, JRJ_00821; EMUS: 1 ♂, JRJ_00736; SDMC: 1 ♂, JRJ_00748, JRJ_00751, JRJ_00795; TAMU: 1 ♀, JRJ_00809; UMMZ: 1 ♀, JRJ_00827); Morelos (EMUS: 7 ♂♂, JRJ_00709, JRJ_00710, JRJ_00711, JRJ_00712, JRJ_00717, JRJ_00731, JRJ_00732; TAMU: 6 ♂♂, JRJ_00719, JRJ_00720, JRJ_00730, JRJ_00737, JRJ_00738, JRJ_00739; UMMZ: 1 ♀, JRJ_00794); Nayarit (EMUS: 2 ♂♂, JRJ_00727, JRJ_00745, 1 ♀, JRJ_00799; FSCA: 1 ♂, JRJ_00754, 3 ♀♀, JRJ_00801, JRJ_00802, JRJ_00803; SDMC: 2 ♂♂, JRJ_00714, JRJ_00722, JRJ_00723, JRJ_00724, JRJ_00725, JRJ_00726, JRJ_00729, JRJ_00740, JRJ_00741, JRJ_00742, JRJ_00743, JRJ_00747, 2 ♀♀, JRJ_00786, JRJ_00787, JRJ_00826); Oaxaca (SDMC: 1 ♂, JRJ_00749); San Luis Potosi (FSCA: 2 ♀♀, JRJ_00785, JRJ_00823; SEMC: 4 ♂♂, JRJ_00721, JRJ_00775, JRJ_00777, JRJ_00778,

JRJ_00824, 5 ♀♀, JRJ_00781, JRJ_00782, JRJ_00797, JRJ_00800, JRJ_00812; TAMU: 2 ♂, JRJ_00718, JRJ_00750; USNM: 1 ♀, JRJ_00793; UMMZ: 1 ♂, JRJ_00774); Sinaloa (CMNH: 1 ♂, JRJ_00764; FSCA: 1 ♀, JRJ_00810, JRJ_00811, JRJ_00813, JRJ_00814, JRJ_00816; SDMC: 1 ♀, JRJ_00792, JRJ_00825; TAMU: 1 ♀, JRJ_00780); Sonora (BYUC: 1 ♂, JRJ_00716); Tamaulipas (EMUS: 1 ♀, JRJ_00784; TAMU: 3 ♀, JRJ_00806, JRJ_00807, JRJ_00808); Querétaro (EMEC: 1 ♀, JRJ_00817; SEMC: 1 ♀, JRJ_00815); Veracruz (CAS: 1 ♂, JRJ_00752; EMEC: 1 ♂, JRJ_00776, 1 ♀, JRJ_00796; EMUS: 1 ♂, JRJ_00733; FSCA: 1 ♂, JRJ_00753; SDMC: 2 ♂♂, JRJ_00713, JRJ_00759; USNM: 1 ♂, JRJ_00735); Yucatan (CLEV: 1 ♂, JRJ_00758; FSCA: 10 ♂♂, JRJ_00756, JRJ_00757, JRJ_00760, JRJ_00762, JRJ_00763, JRJ_00765, JRJ_00766, JRJ_00767, JRJ_00768, JRJ_00772 [A3 Fig. 49], 3 ♀♀, JRJ_00769, JRJ_00771, JRJ_00805); locality uncertain (MHNG: 1 ♂, JRJ_00773, 2 ♀♀, JRJ_00770, JRJ_00804). *Nicaragua*: Matagalpa (SEMC: 1 ♀, JRJ_00839). *Panama*: Chiriqui (MFNB: 1 ♂, JRJ_01630). *Venezuela*: Aragua (CMNH: 1 ♀, JRJ_00888). *Country unknown*: (FMNH: 1 ♀, JRJ_00917).

Morphology, biology and ecology.—This species is broadly distributed, occurring throughout Mexico and Central America with a few records in Brazil and Venezuela. It is very commonly collected and appears regularly at MV and UV light traps. It has also been taken in malaise traps and by beating brush. Collection elevations (as recorded on labels) range from approx. 50 to 1800 m. Collected localities plotted into GoogleEarth revealed sites occurring up to 2100 m.

Discussion.—Van der Weele (1909) characterized the differences between this species and the closely related *flavicornis*, noting that in *angulatus* the wings of females are not darkened, the costal area of the hind wing is often not infuscate, the anal angle of the FW is shorter, and the antennae are darker. Penny (2002) explained that wing infuscation and antennae coloration are highly variable in the two species and are influenced by collection medium, and he synonymized *angulatus* under *flavicornis*. However, there are other important differences between *angulatus* and *flavicornis*, chief among them being wing shape (see discussion for *flavicornis* above).

extensus *species group*

Diagnosis.—*Head*. Vertex setae moderately long, slender, slightly wavy, mixed dark brown and golden yellow. *Thorax*. In males, pronotum posterior flange not developed into an articulating valve. Pleuron with paired oblique pale stripes. *Legs*. Femora of pro- and mesothoracic legs diffusely dusky dark brown on ventral and anterolateral surfaces, tibiae of pro- and mesothoracic legs slightly darker on anterolateral surfaces, all other surfaces pale yellow. *Wings*. Not strongly narrowed at base, HW sometimes narrower overall, particularly in males, apices posteriorly subacute. Pterostigma veinlets and membrane yellow, distal margin of pigment produced two to four cell widths along Sc+R and two to four cell widths along distal margin of wing in apical area, pterostigma thus appearing quite elongate with length more than three times height and distal margin distinctly crescent-shaped. Several species with distinct wing patterns and cell shapes.

Abdomen. Tergum and sternum without distinctive patterning, sometimes posterior margin of each tergite slightly and diffusely darkened, pleural membrane of at least one species sometimes with oblique yellow bands. *Males*. Pleuritocavae visible at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, a second pair sometimes visible at posterior margin of segment 8 but very short. T7 posteromesal margin hood-like, T8 predominately pale yellow, posteromesal and sometimes posterolateral surface with a black maculation, T9 dorsally pale yellow. GPC sometimes slightly everted. Parameres unproduced. *Females*. Interdens present.

Synapomorphies.—male pronotum flange dorsally brown, sublaterally pale, pale areas forming anterior portions of pteronotal sublateral stripes; coxal setae with density and length variable but not very long, pale yellow to yellow on each coxa; basal cell of HW costal area opaque over entire surface, dark reddish brown; FW pterostigma pigment distal margin strongly crescent-shaped, anterior portion following wing margin some distance, posterior portion with a short piece following along Sc+R one or two cell lengths; pleural membrane evenly brown.

Discussion.—This group has very similar male genitalia to the *flavicornis* species group and with it forms a monophyletic lineage (See A3 Fig. 1 node 32). Synapomorphies uniting the two species groups include the following: clypeus dorsolaterally with vague diffuse darkening or very small incipient or vestigial maculations; males with T7 ventral and T8 dorsal surfaces distinctly and completely or nearly completely cream or yellow.

Haploglenius extensus *Banks, 1924*

(A3 Figs. 51–52, 90)

Haploglenius extensus Banks, 1924

—Banks 1924.01.?? r#76: 437 {OD: ♀, D. TS: not indicated [holotype by monotypy]. TL: “Bolivia, Sara”. TR: MCZ. Type specimen not examined (see “Discussion” below).}

—Penny 1978.09.15 r#5098: 13 {GD, L}

—Ábrahám 2013.04.30 r#?????: 185 {DIS, GD, L, SYN, TL, TR, TS}

Verticillecerus extensus (Banks, 1924)

—Ábrahám 2013.04.30 r#?????: 185 {SYN}

<u>Etymology and nomenclatural notes</u>.—extensus: alternate form of extentus (Latin) ‘stretched, extended, enlarged, increased’. Apparently named for the prolonged apical margin of the pterostigma pigment: “the stigma…with a slight extension”.

Diagnosis.—Parasagittal stripes present, usually well-expressed. Pterostigma yellow, produced along margin in apical area. Cells subtending R not enlarged, margined, margining collectively forming an infuscate stripe reaching to pterostigma and continuing past it into apical area. HW slightly narrower than in *cuboides*. HW anal area with two fully developed rows of cells, posterior (marginal) row often with numerous cells divided by crossveins. Lateral areas of abdominal tergites often paler to yellowish, sometimes forming a diffuse longitudinal pale stripe along length of abdomen.

Autapomorphies.—antennae with verticils on mesal surface of nodes of first three or four flagellomeres, approximately coequal in length with a single flagellomere; male HW basiposterior margin weakly convex, narrowing slightly at Mp_1; cells subtending R in radial area thickly margined, and intercalary cells, when present, completely filled with pigment.

Distribution.—Central Bolivia: Santa Cruz, Sara.

Description.—

Size (mm). Male: length of body 23–34, abdomen 16–25, forewing 32–40, hind wing 28–35, antennae 22–27. Female: length of body 33–34, abdomen 23–24, forewing 44–46, hind wing 39–41, antennae 25–26.

Head. Breadth at widest point (of eyes) slightly subequal to width of mesothorax at wing base with wings folded back. Occiput with pattern variable and irregular, with diffuse blotches of yellow and brown. Vertex pale to dark sandy reddish brown; setae somewhat sparse, moderately long, slender, slightly wavy, mixed dark brown and golden yellow. Extra-torular sclerites concolorous with upper portion of frons. Paraocular band dusky dark brown near antennae, dusky dark orangish or reddish brown laterad of frons, narrowly pale orangish or yellowish along orbital sclerite. Frons very pale to dark brown; setae moderately dense, moderately long, slender, golden, transitioning to dark brown laterally. Clypeus yellow, occasionally laterally with small diffuse reddish brown maculations. Labrum concolorous with clypeus. Mandibles pale yellow basally, apices dark reddish brown. Labium pale amber yellow, a thin diffuse dark brown sagittal line present. Eyes very slightly dorsoventrally oblong. Antennae flagellomeres slightly swollen at nodes, antennae coloration somewhat variable, flagellum pale brownish or reddish yellow, nodes paler, verticils absent; clubs fusiform, apices distinctly acuminate, pale yellow, entire flagellum and club sometimes slighty darker on dorsal surface, covered in fine dark setae.

Thorax. Cervix. Dorsal cervical plate setae golden. Cervical sclerite dark brown. *Pronotum.* Anterior flange somewhat narrow, somewhat produced dorsad. Posterior flange of females not quite covering mesacrotergite, in males only very barely covering mesacrotergite, white crystalline material absent. Pronotum base color dark brown, a yellow longitudinal stripe beginning sublaterally on anterior flange and continuing to posterior margin of posterior flange and onto pteronotum. All surfaces with moderately long, very fine, brown setae. *Pteronotum*. Evenly dark earthy brown, a yellow sublateral longitudinal stripe running from lateral surface of mesoprescutum, posteriorly on scutum, onto scutellum, and continuing onto metascutum and metascutellum; velvety spots of metascutum dark reddish brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, mixed golden brown and very pale yellow, stripes with pruinescence.

Legs. Femora of pro- and mesothoracic legs diffusely dusky dark brown on ventral and anterolateral surfaces, tibiae of pro- and mesothoracic legs slightly orangish on anterolateral surfaces, all other surfaces pale yellow; tarsi dark reddish brown to almost black, terminal tarsomere pale reddish or orange in distal two-fifths. Coxae setae very pale to white; antennal comb setae golden.

Wings. Dimension and shape. Long, slender, especially HW, apex posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, width of cells more or less coequal to height, cells narrowing slightly near pterostigma. Pterostigma with five to six forked and unforked pale yellow veinlets, occasionally tinged with brown; membrane pale yellow, slightly translucent to distinctly opaque, distal margin of pigment produced two to three cell widths along Sc+R and two to four cell widths along distal margin of wing in apical area, pterostigma thus appearing quite elongate with length more than three times height and distal margin distinctly crescent-shaped. Deltus medium to dark brown, translucent to opaque. Presectoral area with ca. eleven to twelve cells. Rs with ca. six forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. eleven to thirteen irregular to more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin slightly concave, anal angle slightly developed, not yet tooth-like, a single cell row distad of Cup + 1a, occasionally a few distal cells divided by crossveins. *Color and patterning.* Venation colorations as follows: C and Sc veinlets pale yellow, R dark brown, Mp basally pale yellow, all other veins, veinlets, and crossveins pale to dark brown. Costal and subcostal areas weakly fuscous, with pigment narrowly absent along anterior margin of costal cells, subcostal veinlets diffusely margined. Presectoral and radial area with anterior portions of cells in row subtending R tinted brown, forming, with costal and subcostal area pigment, a stripe from wing base to apical area. Apical area fuscous, darkest anteriorly, posterad of pterostigma. Some specimens with entire wing membrane weakly tinged with brown. HW. As in forewing except as follows. Mp_2 fork angle less than 90°. Medial triangle distal domain with one to two cells, very slightly longer in males. Pre-Cup axillary disk dark brown, becoming yellow posteriorly. Pre-Mp_1 area margin unexpanded, more reduced in females. Anal area with two rows of cells, but marginal row often divided by irregular crossveins, giving the appearance of a partial to nearly complete third row.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Medium to dark earthy brown, lateral areas of tergites often paler to yellowish, sometimes forming a diffuse longitudinal pale stripe along length of abdomen, sometimes posterior margin of each tergite slightly and diffusely darkened; T1 and T2 with moderately dense, long, wispy, golden brown setae, remainder of tergum devoid of long setae. *Sternum*. S1 to S2 more or less orange to yellowish with a thin sagittal brown line, S3 to S4 often with diffuse irregular blotches of yellow, remaining sternites variably brown to somewhat diffusely yellowish; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, sometimes with areas of irregular yellowish pigment; devoid of long setae.

Male terminalia. Unmacerated specimens. Somewhat small pleuritocavae visible at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, a second pair often visible at posterior margin of segment 8 but very short, T7 posteromesal margin hood-like, T8 predomintely pale yellow, posteromesal surface with a black maculation, T9 dorsally pale yellow, GPC slightly everted, pulvini not visible, ectoprocts dark brown, yellow dorsally, S9 dark brown. *Macerated specimens.* Pleuritocavae medium length, a few times longer than width at base, surface convoluted with a dense coat of microsetae, length of pleuritocava of segment 8 short, less than one-fourth that of segment 7. S9 apical margin obtusely angled, nearly acute. Pulvini somewhat small, very weakly sclerotized, length about coequal to width at base, bearing several very long, slender, brown setae. GPC somewhat sclerotized; in lateral view dorsal margin somewhat raised in basal half, mesally distinctly notched, ventrally more or less entire, dorsal and ventral margins subparallel; in ventral view somewhat broad basally, lateral margins evenly rounded and converging apicad. Parameres in ventral view with anterolateral margin slightly irregular, lateral margins weakly differentiated. Pelta weakly sclerotized, almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae dull reddish brown, distivalvae yellow, ectroprocts brownish orange. *Macerated specimens.* Ventrovalvae in lateral and ventral views somewhat elongate and narrow, length ca. two times width, with setae moderately long and rather robust, more so than in other species. Distivalvae setae also slightly longer and more robust, but not as long and robust as on ventrovalvae. Linguella undifferentiated from surrounding membrane, unsclerotized, bearing several short, very slender, very pale setae. Interdental space small, more or less round. Interdens sclerotized, round at base, short, cone-shaped.

Variation. Notal stripes very slender and well defined in some specimens, slightly wider and more diffuse in others. Lateral stripes of abdominal tergum well developed in some specimens, but poorly developed in others.

Type material examined.—Not available for this study.

Additional material examined.—*Bolivia*: Santa Cruz (CMNH: 1 ♀, JRJ_00918; FSCA: 5 ♂♂, JRJ_00599 [A3 Fig. 51], JRJ_00600, JRJ_00603, JRJ_00604, JRJ_00605, 3 ♀♀, JRJ_00601, JRJ_00602, JRJ_00606 [A3 Fig. 52]; USNM: 1 ♂, JRJ_00607).

Morphology, biology and ecology.—Specimens were collected at UV, MV and incandescent lights.

Discussion.—Banks' (1924) description, though brief, provides enough information to match it confidently to material available for this study (i.e., thorax stripes, elongate pterostigma, wing stripe, long narrow HW wing, distribution).

The handful of specimens examined were all collected from a very narrow location, but by several different collectors on different dates.

Haploglenius cuboides *new species*

(A3 Figs. 53–54, 90)

Etymology and nomenclatural notes.—*cuboides*: cubus (Latin) +-oides (Latin), 'like, having the form of', = 'cube-like'. Refers to the squarish cells subtending R; their shape is common in many species, but in this species they are anterolaterally margined and rather distinctive.

Diagnosis.—Pteronotum parasagittal stripes usually present in females, sometimes weakly expressed, absent in males examined. Pterostigma yellow, produced along margin in apical area two to four cell widths. HW slightly broader than in *extensus*. HW anal area with three fully developed rows of cells. Cells subtending R not enlarged, their height and width co-equal, narrowly anterolaterally margined, accentuating cells' cube-like shape. T7 hood-like, small pleuritocavae visible at posterior margin of T7 pleural membrane.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Brazil: Rôndonia.

Description.—

Size (mm). Male: length of body 36, abdomen 25, forewing 42–43, hind wing 38–39, antennae 28–29. Female: length of body 27–35, abdomen 23–24, forewing 44–51, hind wing 39–46, antennae 26–27.

Head. Occiput with pattern variable and irregular, color predominately yellow laterad, proximally brown. Vertex sandy reddish brown; setae somewhat sparse, moderately long, slender, slightly wavy, mixed dark and golden brown. Extra-torular sclerites concolorous with upper portion of frons. Paraocular band dusky dark brown near antennae, dusky dark orangish or reddish brown laterad of frons, somewhat broadly pale orangish or yellowish along orbital sclerite. Frons pale to rather dark dusky orange, transitioning to medium to dark brown on prefrons; setae moderately dense, long, slender, golden, transitioning to dark brown dorsolaterally. Clypeus yellow or orangish, occasionally laterally with diffuse reddish brown maculations. Labrum more or less concolorous with mesal portion of clypeus. Mandibles pale yellow basally, apices dark reddish brown. Labium rather flimsy, often folded or discolored in pinned specimens, amber to reddish yellow, a thin dark brown sagittal line weakly expressed. Eyes very slightly dorsoventrally oblong, very slightly larger in ventral half. Antennae flagellomeres slightly swollen at nodes, antennae coloration somewhat variable, flagellum reddish brown, paler on anterior surface, nodes thinly pale, verticils absent; clubs elongate, asymmetrical and somewhat fusiform, apices distinctly acuminate, anteroventrally brown, dorsoposteriorly pale yellow, sometimes pale surface divided by a longitudinal diffuse brown line, covered in fine pale golden setae.

Thorax. Cervix. Dorsal cervical plate setae pale golden. Cervical sclerite dark brown. *Pronotum.* Anterior flange somewhat narrow, slightly produced dorsad, weakly bilobed. Posterior flange of females not quite covering mesacrotergite, in males only very barely covering mesacrotergite, white crystalline material absent. Pronotum base color medium to dark brown, in females a moderately narrow yellow longitudinal stripe beginning sublaterally on anterior flange and continuing to posterior margin of posterior flange and onto pteronotum, in males stripes essentially absent. All surfaces with moderately long, very fine, golden brown setae. *Pteronotum.* Evenly medium to dark earthy brown, in females a narrow yellow sublateral longitudinal stripe running from lateral surface of mesoprescutum, posteriorly on scutum, and sometimes onto scutellum, in males stripes essentially absent; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, mixed pale yellow and golden, stripes often with pruinescence.

Legs. Femora of pro- and mesothoracic legs diffusely dusky dark brown on ventral and anterolateral surfaces, tibiae of pro- and mesothoracic legs dusky brown on anterolateral surfaces, all other surfaces predominately pale yellow, sometimes with narrow diffuse areas of dusky brown pigment; tarsi dark reddish brown to almost black, terminal tarsomere pale reddish or orange in distal one-third. Coxae setae pale yellow; antennal comb setae copper colored.

Wings. Dimension and shape. Long, moderately slender, apex posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, cells wide, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with four to six forked and unforked pale yellow veinlets, occasionally tinged with brown; membrane pale yellow, translucent, distal margin of pigment produced one to two cell widths along Sc+R and two to four cell widths along distal margin of wing in apical area, pterostigma thus appearing quite elongate with length more than four times height and distal margin distinctly crescent-shaped. Deltus medium to dark brown, translucent. Presectoral area with ca. nine to eleven cells. Rs with ca. six to seven forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. eleven to thirteen irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin essentially straight, often very slightly concave or very slightly convex, anal angle not developed, cell row distad of Cup + 1a divided in distal two-thirds by oblique crossveins and thus appearing as two mostly complete but irregular rows. *Color and patterning.* Venation medium to dark brown. Costal and subcostal areas fuscous, subcostal veinlets diffusely margined. Apical area fuscous, darkest anteriorly, posterad of pterostigma. Some specimens with entire wing membrane weakly tinged with brown. HW. As in forewing except as follows. Mp_2 fork angle less than 90°. Medial triangle distal domain with two to four cells, very slightly longer in males. Pre-Cup axillary disk dark brown. Pre-Mp_1 area margin unexpanded in females, expansion very slight and broad in males. Anal area with three complete rows of cells.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly brown, posterior margin of each tergite diffusely darkened; T1 and T2 with moderately dense, long, wispy golden setae, remainder of tergum devoid of long setae. *Sternum*. More or less medium to dark brown, S1 and S2 diffusely yellowish laterally, ventral surface of sternites sometimes diffusely yellowish; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, sometimes with ca. three to four faint oblique yellow bands; devoid of long setae.

Male terminalia. *Unmacerated specimens.* Somewhat small pleuritocavae visible at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, T7 posteromesal margin weakly hood-like, T8 predomintely pale yellow, posteromesal surface with a large black maculation, T9 dorsally pale yellow, GPC not everted, pulvini not visible, ectoprocts and S9 dark brown. *Macerated specimens.* Pleuritocavae somewhat small, a few times longer than width at base, surface convoluted with a dense coat of microsetae, length of pleuritocava of segment 8 very short, one-third to one-half that of segment 7. S9 apical margin obtusely angled. Pulvini somewhat small, very weakly sclerotized, length about coequal to width at base, bearing several very long, somewhat slender, brown setae. GPC somewhat sclerotized; in lateral view dorsal margin somewhat raised in basal half, mesally distinctly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view somewhat broad basally, converging apicad, with a undulating lateral margin. Parameres in ventral view with anterolateral margin slightly irregular, proximolateral margins rather well differentiated. Pelta sclerotized, narrowly almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae and distivalvae yellowish to medium brown, ectroprocts brown, proximomesal area of lateral surface pale. *Macerated specimens.* Ventrovalvae in lateral and ventral views somewhat elongate and narrow, length ca. two times width. Linguella only weakly differentiated from surrounding membrane, unsclerotized, bearing several short, stiff, slender, pale setae. Interdental space small, more or less round. Interdens sclerotized, round at base, short, cone-shaped.

Variation. Specimen JRJ_00608, a male, with incipient pteronotal stripes, the sublateral surfaces being somewhat pale.

Type material examined.—*Holotype* (A1 Fig. 54), **new designation**, female, Brazil, in FSCA collection: "BRAZIL: Rondônia. 62 km SW Ariquemes, nr Fzda. Rancho Grande 5-17-X-1993 JE Eger MV & Black Lights /// HOLOTYPE Haploglenius cuboides Jones ♀ design. J. R. Jones 2014 /// JRJ_00616". Condition: excellent; antennae and wings spread, no parts missing.

Additional material examined.—*Brazil*: Rondônia (FSCA: 2 ♂♂, JRJ_00608, JRJ_00618, 5 ♀♀, JRJ_00610, JRJ_00611, JRJ_00612, JRJ_00614, JRJ_00619; TAMU: 1 ♂, JRJ_00609 [A3 Fig. 53]; UCDC: 2 ♀♀, JRJ_00613, JRJ_00617).

Morphology, biology and ecology.—Most of the specimens collected were taken at MV and UV lights.

Discussion.—All known specimens of this species were collected at the same locality, a ranch in Rondônia, but by different collectors and on different dates.

Haploglenius decorus *Ábrahám, 2013*

(A3 Figs. 55, 90)

Haploglenius decorus Ábrahám, 2013

—Ábrahám 2013.04.30 r#?????: 179, figs. 7–9 {OD: ♂♀, BIO, D, ET, GD, MOR. TS: holotype by original designation. TL: "Guyane French NW 20 km of St. Laurent du Maroni route Crique NAI". TR: SCMK. Type specimen not examined (see "Discussion" below).}

Etymology and nomenclatural notes.—*decorus*: decorus (Latin), 'fitting, proper, beautiful'. Ábrahám states "decorus means beautiful".

Diagnosis.—Pterostigma yellow, produced along margin in apical area one to two cells widths and along Sc+R. HW anal area with three fully developed rows of cells. Presectoral area with ca. six to seven irregular cells. Cells subtending R enlarged, width of mesal-most cells >3x height, with ventral margins highly irregular, laterally separated from one another by small intercalary cells. Anterolateral margins of cells heavily margined, giving cell row a reticulate or net-like appearance. T7 margin of males hood-like, segment 7 pleuritocavae moderately long.

Autapomorphies.—male pronotum flange dorsally evenly medium brown; FW intercalary cells present; FW subcostal area undulations pigmented, forming distinct pseudoveinlets.

Distribution.—Coastal French Guiana.

Description.—

Size (mm). Male: length of body 31, abdomen 22, forewing 38–39, hind wing 32–33, antennae 23.

Head. Occiput predominately reddish brown with some faint irregular pale maculations. Vertex medium sandy reddish brown; setae moderately dense, moderately long, slender, slightly wavy, mixed dark and golden brown. Extra-torular sclerites dark reddish brown. Paraocular band dusky dark brown near antennae, slightly paler laterad of frons, transitioning to yellowish laterad of ventral portion of frons, orbital sclerite often thinly pale. Frons dusky dull orange, becoming narrowly slightly darker dorsad near prefrons; setae moderately dense, moderately long, slender, golden mesally, otherwise dark brown. Clypeus yellow, laterally very faintly darkened. Labrum concolorous with clypeus. Mandibles pale yellow basally, apices dark reddish brown.

Labium pale amber yellow, a thin incomplete reddish brown sagittal line present. Eyes slightly dorsoventrally oblong, a hint of posteromesal flattening. Antennae flagellomeres slightly swollen at nodes, flagellum reddish brown, slightly paler on anterior surface, nodes narrowly pale, verticils absent; clubs asymmetrically elongate pyriform, apex acuminate, mostly brown, posterior surface pale yellow, covered in fine golden brown setae.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite dark brown. *Pronotum.* Anterior flange somewhat narrow, somewhat produced dorsad, weakly bilobed. Posterior flange not quite covering mesacrotergite, white coating absent. Pronotum coloration evenly dark brown. All surfaces with moderately long, very fine, golden brown setae. *Pteronotum*. Evenly medium to dark earthy brown, lateral surfaces of mesoprescutum narrowly yellow; velvety spots of metascutum dark reddish brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes with somewhat diffuse margins descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, pale golden yellow, stripes with pruinescence.

Legs. Femora of pro- and mesothoracic legs diffusely dusky dark brown on ventral and anterolateral surfaces; femora of metathoracic leg slightly dusky brown on anterolateral surface; tibiae of pro- and mesothoracic legs slightly light dusky brown on anterolateral surfaces, all other surfaces pale yellow; tarsi dark reddish brown to almost black, terminal tarsomere pale reddish or orange in distal two-fifths. Coxae setae yellow; antennal comb setae coppery gold.

Wings. Dimension and shape. Rather long and slender, posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, width of cell variable, width of at least several cells more than two times height, but many cell with width more or less coequal to height, cells narrowing somewhat in distal half of wing. Pterostigma with ca. five forked and unforked pale yellow veinlets, sometimes slightly tinted brown; membrane cream yellow, opaque, distal margin of pigment produced one to two cell widths along Sc+R and one to two cell widths along distal margin of wing in apical area, pterostigma thus appearing somewhat elongate with length three times height and distal margin distinctly crescent-shaped. Deltus medium to dark brown, sometimes darkening anteromesally, translucent to opaque. Presectoral area with ca. six to seven irregular cells, these sometimes divided by irregular secondary veinlets. Cells subtending R significantly enlarged and broadened, width of several of these cells two and a half to four times height, margin shape highly irregular, with at least some of the large cells flanked by small irregular intercalary cells. Rs with ca. five forks, the first few forks highly irregular as they track the ventral margins of the enlarged cells subtending R. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. seven to nine often highly irregular rows of cells. Cubital triangle distal domain with two cells. Anal area hind margin essentially straight, often very slightly concave or very slightly convex, anal angle essentially undeveloped, cell row distad of Cup + 1a with several cells in distal two-thirds divided by oblique crossveins and thus appearing as two partially complete and irregular rows. *Color and patterning.* Venation medium to dark brown. Costals posterolaterally broadly and diffusely margined, nearly filling cells but leaving a small gap anteromesally, subcostal area fuscous. Presectoral and radial area with lateral crossveins of cells subtending R broadly margined with pigment, giving these large cells a reticulate appearance. Apical area weakly fuscous, pigment becoming darker near pterostigma and margining cells along Sc+R. Entire wing membrane weakly tinged with brown. HW. As in forewing except as follows. Pterostigma veinlets brown or yellow and heavily tinged with brown. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with one to two cells. Pre-Cup axillary disk dark brown. Pre-Mp_1 area margin only very weakly expanded. Anal area with three complete rows of cells.

Abdomen. Not quite reaching to pterostigma with wings folded back. *Tergum*. Evenly brown, sometimes posterior margin of each tergite slightly and diffusely darkened; T1 and T2 with moderately dense, long, wispy, golden brown setae, remainder of tergum devoid of long setae. *Sternum*. S1 often mostly yellow, S2 variable, often brown and laterally yellowish, S3 sometimes proximally diffusely yellowish, sternum otherwise more or less evenly brown, sometimes with very faint yellowish areas; mostly devoid of long setae, some moderately long, wispy golden setae on S1 and S2. *Pleural membrane*. Dark brown, devoid of long setae.

Male terminalia. Unmacerated specimens. Moderately long pleuritocavae present, visible or not at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, a second smaller pleuritocava present, visible or not, at posterior margin of segment 8, T7 posteromesal margin hood-like, T8 predominately pale yellow, distolateral and distomesal surfaces diffusely black, T9 dorsally pale yellow, GPC not everted, pulvini not visible, ectoprocts dark brown, yellow dorsally and laterally, S9 dark brown. *Macerated specimens.* Pleuritocavae a few times longer than width at base, surface convoluted with a dense coat of microsetae, length of pleuritocava of segment 8 short, less than half that of segment 7. S9 apical margin obtusely angled, nearly acute. Pulvini somewhat small, very weakly sclerotized and weakly differentiated from gonosaccal membrane but slightly produced, bearing many long, very slender, brown setae. GPC somewhat sclerotized; in lateral view dorsal margin somewhat raised in basal half, mesally distinctly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view somewhat broad basally, lateral margins undulating. Parameres in ventral view with anterolateral margin subangulate, posterolateral margins somewhat well differentiated. Pelta weakly sclerotized, almond shaped.

Female terminalia. Adapted from Ábrahám's (2013) description and figure: Ventrovalvae in lateral view elongate and narrow, with setae moderately long and rather robust, more so than in other species. Distivalvae setae also slightly longer and more robust. Linguella slightly sclerotized, bearing short brown setae. Interdens not visible [probably present, but small and cone-shaped as in pther related species].

Variation. Specimen JRJ_01629 (A3 Fig. 55) with coloration of lateral surfaces of mesoprescutum essentially undifferentiated from remainder of pteronotum, entire dorsal surface essentially medium dark brown. Enlarged cells subtending R highly variable in shape. The pterostigma apical margins are not as distinctly crescent shaped as other species in this species group.

Type material examined.—Not available for this study.

Additional material examined.—*French Guiana*: Cayenne (FSCA: 1 ♂, JRJ_00628; MNHN: 1 ♂, JRJ_01629 [A3 Fig. 55]).

Morphology, biology and ecology.—Nothing is known about the biology of this species.

Discussion.—Ábrahám (2013) thought that specimens with the reticulated wing pattern from Ecuador to French Guiana represent a single species, but specimens in French Guiana have several unique features which differentiate them from those in the central and western parts of the range, including fewer presectoral cells (six to seven, versus seven to ten in western specimens) and a few to several intercalary cells. The central and western specimens represent a new species described below as *decoratus*.

Haploglenius decoratus *new species*

(A3 Figs. 56–57, 90)

[*Haploglenius decorus*, Ábrahám 2013]

—Ábrahám 2013.04.30: 179 {male paratype of *Haploglenius decorus* from Ecuador}

Etymology and nomenclatural notes.—*decoratus*: decoratus (Latin), ‘adorned, graced, beautified’. Named for the dramatic patterning of the cells subtending R, and also allusive to the similar species *decorus* Ábrahám.

Diagnosis.—Pteronotum often with very thin and rather weakly expressed parasagittal stripes. Sc veinlets yellow. Pterostigma yellow, produced along margin in apical area two to three cell widths. HW anal area with three fully developed rows of cells. Presectoral area with ca. seven to ten sometimes irregular cells, these sometimes divided by secondary veinlets. Cells subtending R enlarged with irregular ventral margins, usually without, occasionally with very few, smaller intercalary cells. Expression of margining pattern variable, from very reduced (often in females) to heavily margined and distinctive (often in males). T7 of males hood-like, pleuritocavae moderately long.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Brazil, Ecuador, Peru.

Description.—

Size (mm). Male: length of body 32–38, abdomen 23–26, forewing 38–44, hind wing 34–38, antennae 23–26. Female: forewing 46, hind wing 41–44, antennae 27.

Head. Occiput with pattern variable and irregular, with diffuse blotches of yellow and brown. Vertex pale to dark sandy reddish brown; setae often slightly denser on anterior surface, moderately dense to somewhat sparse overall, moderately long, slender, slightly wavy, mixed dark and golden brown. Extra-torular sclerites dark reddish brown, sometimes laterally paler. Paraocular band dark brown near antennae, brown laterad of frons, orbital sclerite often thinly yellow or pale. Frons dusky pale to dark yellowish, becoming narrowly darker dorsad near prefrons, which is also dusky brown; setae moderately dense, moderately long, slender, brown. Clypeus yellow, occasionally laterally with small diffuse reddish brown maculations. Labrum concolorous with clypeus. Mandibles pale yellow basally, apices dark reddish brown. Labium pale amber yellow, a thin diffuse dark brown sagittal line present. Eyes very slightly dorsoventrally oblong. Antennae flagellomeres slightly swollen at nodes, antennae coloration somewhat variable, flagellum dorsally reddish brown, ventrally pale yellowish brown, nodes narrowly pale, verticils absent; clubs at least somewhat elongate pyriform, apices weakly acuminate, brown, pale yellow on one surface, entire flagellum and club sometimes slightly darker on opposing surface, covered in fine golden brown setae.

Thorax. *Cervix*. Dorsal cervical plate setae golden brown. Cervical sclerite dark brown. *Pronotum*. Anterior flange somewhat narrow, somewhat produced dorsad, weakly bilobed. Posterior flange not quite covering mesacrotergite, white coating absent, males and females essentially identical. Pronotum base color dark brown, a yellow longitudinal stripe beginning sublaterally on anterior flange and continuing to posterior margin of posterior flange and onto pteronotum, sometimes weakly expressed on posterior flange. All surfaces with moderately long, very fine, golden brown setae. *Pteronotum*. Evenly medium to dark earthy brown, a yellow sublateral longitudinal stripe running from lateral surface of mesoprescutum, posteriorly on scutum, onto scutellum, not continuing onto metanotum; velvety spots of metascutum dark reddish brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, pale yellow with some golden setae mixed in, stripes sometimes with pruinescence.

Legs. Femora of pro- and mesothoracic legs diffusely dusky dark brown on ventral and anterolateral surfaces; femora of metathoracic leg slightly dusky brown on anterolateral surface; tibiae of pro- and mesothoracic legs slightly light dusky brown on anterolateral surfaces, all other surfaces pale yellow; tarsi dark reddish brown to almost black, terminal tarsomere pale reddish or orange in distal two-fifths. Coxae setae very pale to white; antennal comb setae golden yellow.

Wings. Dimension and shape. Long, slender, HW narrowing somewhat in distal two-thirds, apex posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, width of cells more or less coequal to height, cells narrowing slightly near pterostigma. Pterostigma with six to seven forked and unforked yellow veinlets; membrane pale yellow, sometimes faintly tinged with reddish pigment, slightly translucent to distinctly opaque, distal margin of pigment produced two to three cell widths along Sc+R and two to three cell widths along distal margin of wing in apical area, pterostigma thus appearing quite elongate with length more than three times height and distal margin distinctly crescent-shaped. Deltus medium to dark brown, sometimes darkening anteromesally, translucent to opaque. Presectoral area with ca. seven to ten sometimes irregular cells, these sometimes divided by secondary veinlets. Cells subtending R significantly enlarged and broadened, margin shape irregular, but cells more or less similar in size and shape, with zero to two intercalary cells, usually none. Rs with ca. six sometimes irregular forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine to thirteen irregular to more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin essentially straight, often very slightly concave or very slightly convex, anal angle essentially undeveloped, cell row distad of Cup + 1a divided in distal two-thirds by oblique crossveins and thus appearing as two mostly complete but irregular rows. *Color and patterning.* Venation colorations as follows: Sc veinlets yellow, all other veins, veinlets, and crossveins medium to dark brown. Costal and subcostal areas weakly fuscous, with pigment narrowly absent along anterior margin of costal cells, subcostal veinlets often appearing diffusely margined. Presectoral and radial area with lateral crossveins of cells subtending R often margined with brown pigment, this pigment somewhat paler in available females and some males. Apical area often completely fuscous, darkest anteriorly, just posterad of pterostigma. Some specimens with entire wing membrane weakly tinged with brown. HW. As in forewing except as follows. Mp_2 fork angle less than 90°. Medial triangle distal domain with one to two cells, very slightly longer in males. Pre-Cup axillary disk dark brown. Pre-Mp_1 area margin essentially unexpanded, slightly more reduced in females. Anal area with three complete rows of cells.

Abdomen. In males not quite reaching to pterostigma with wings folded back; in available females abdomens missing. *Tergum*. Medium to dark earthy brown, sometimes posterior margin of each tergite slightly and diffusely darkened; T1 and T2 with moderately dense, long, wispy, golden brown setae, remainder of tergum devoid of long setae. *Sternum*. S1 often mostly yellow, S2 variable, often brown and laterally yellowish, S3 sometimes proximally diffusely yellowish, sternum otherwise more or less evenly brown, sometimes with very faint yellowish areas; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown; devoid of long setae.

Male terminalia. Unmacerated specimens. Moderately long pleuritocavae present, visible or not at posterior margin of pleural membrane of segment 7, wrinkled, very dark brown dorsally, yellowish or pale ventrally, a second smaller pleuritocava present at posterior margin of segment 8, T7 posteromesal margin hood-like, T8 predominately pale yellow, distimesal surface with a black maculation, T9 dorsally pale yellow, GPC not everted, pulvini not visible, ectoprocts dark brown, yellow dorsally and laterally, S9 dark brown. *Macerated specimens.* Pleuritocavae variable in length, a few times longer than width at base, corkscrewing or not, surface convoluted with a dense coat of microsetae, length of pleuritocava of segment 8 short, less than half that of segment 7. S9 apical margin obtusely angled, nearly acute. Pulvini somewhat small, very weakly sclerotized, length very slightly greater than width at base, bearing several long, very slender, brown setae. GPC somewhat sclerotized; in lateral view dorsal margin somewhat raised in basal half, mesally distinctly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view somewhat broad basally, lateral margins weakly undulating. Parameres in ventral view with anterolateral margin slightly irregular, somewhat blunt, lateral margins somewhat well differentiated. Pelta weakly sclerotized, almond shaped.

Variation. Notal longitudinal stripes poorly developed to absent in some individuals (JRJ_00631, JRJ_00632, males from Brazil; JRJ_01640 [A3 Fig. 56], a male from Peru), other males and females have the stripes more or less complete but variable; often very thin or faint. The two available females are overall very pale in the intensity of wing maculation; some of the males are also pale. At least one male (JRJ_00632) has the wing maculation very dark and intense.

Type material examined.—*Holotype*, **new designation**, male, Brazil, in INPA collection: “BRASIL, AM, Pr. Figueiredo Rod. 240, km-24, Ramal São Francisco 29-

31.x.2008 /// J.A. Rafel, F.F. Xavier F°, G. Lourido, R.J.P. Machado & E. Amat, arm. luz solo /// HOLOTYPE Haploglenius decoratus Jones ♂ design. J. R. Jones 2014 /// JRJ_00632”. Condition: excellent; antennae and wings spread, left hind leg missing.

Additional material examined.—*Brazil*: Amazonas (INPA: 1 ♂, JRJ_00631); Para (INPA: 1 ♂, JRJ_00633); locality uncertain (MFNB: 1 ♀, JRJ_01752 [A3 Fig. 57]). *Peru*: Huanuco (FSCA: 1 ♀, JRJ_00630; SEMC: 1 ♂, JRJ_00629); San Martin (BMNH: 1 ♂, JRJ_01640 [A3 Fig. 56]).

Morphology, biology and ecology.—Specimens in loan material were collected at elevations of 85 to ca. 700 m. Two were recording as having been collected at lights, one with mercury vapor.

Discussion.—This species is very similar to *decorus* Ábrahám, especially in the expression of the unique reticulated wing pattern of males. Ábrahám (2013) considered all specimens with the pattern to be conspecific, his concept comprising individuals distributed from Ecuador to French Guiana, but there are distinct differences between the specimens occurring through most of this range and those in French Guiana. From material available for this study and that presented by Ábrahám , Ábrahám’s *decorus* constitutes only specimens occurring in coastal French Guiana (five of the six specimens he examined), although the true range may extend further west and south. The new species *decoratus* has a much broader range (see A3 Fig. 90).

There is some variation in the *decoratus* specimens in the size and shape of the cells subtending R and in the expression of their patterning. Some specimens (both males and females) have at least some of the largest cells slightly wider (ca. 3x height), whereas in others the largest cells are less wide (ca. 2x height). One male from Peru (JRJ_01640 [A3 Fig. 56]) has a few intercalalery cells beginning to form. Several males have the margining of the cells quite dark, but in others the pattern is paler; in the two females examined the pattern is evident but the margining thin and pale, and in this regard they look rather similar to *cuboides*.

***Species not placed within species groups of* Haploglenius**

Discussion.—Several species of *Haploglenius* were not placed in the cladistic analysis within one of the well-defined species groups. These stem species are decribed below.

Haploglenius procerus *new species*

(A3 Figs. 58, 91)

Etymology and nomenclatural notes.—*procerus*: procerus (Latin), ‘extended, elongated’. Named for the long distal domain of the medial triangle in the HW.

Diagnosis.—Pterostigma pigment yellow, distal margin of pigment very slightly crescent-shaped. Wing apices diffusely infuscate. FW hind margin distad of anal angle convex. FW anal area cell row with several cells in distal half divided by oblique crossveins. HW anal area with three well-developed rows of cells. Distal domain of medial triangle length >2.5x width at base, comprising two to five often narrowed cells. Males: Pronotal valve well-developed. Acrotergite simple, not bilobed. Pleuritocavae absent.

Autapomorphies.—FW anal area with a single row of cells roughly parallel to Cua, not split by crossveins; male HW distal domain very elongate and narrow, with three or more cells.

Distribution.—Costa Rica, Honduras, Panama.

Description.—

Size (mm). Male: length of body 37–44, abdomen 27–31, forewing 38–44, hind wing 32–38, antennae 21–25. Female: length of body 28–39, abdomen 19–28, forewing 45–50, hind wing 38–44, antennae 22–26.

Head. Occiput with irregular diffuse brown patterning, a small diffuse yellow macula along margin near vertex. Vertex brown; setae moderately dense, moderately long, brown. Extra-torular sclerites dark brown. Paraocular band dusky dark brown dorsally, transitioning to orangish or dusky yellow ventrally. Frons dull yellow, dorsolaterally narrowly and diffusely dusky brownish (prefrontal area dark dusky brown), sometimes diffusely dark brown sagittally; setae moderately dense, yellowish, dark brown dorsolaterally. Clypeus yellow. Labrum concolorous with clypeus. Mandibles dull yellow basally, transitioning to very dark reddish brown apically. Labium concolorous with labrum, with a thin brown sagittal line. Eyes in anterior view dorsally only very slightly enlarged, in lateral view very slightly dorsoventrally oblong, with only a very faint dorsoventral mesal division. Antennae flagellomeres very slightly swollen at nodes, flagellum brown, nodes narrowly pale brown; clubs slightly elongate pyriform, dark brown, anteriorly yellowish, yellow region divided by a diffuse sagittal brown stripe, covered in fine dark setae; verticils absent.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite evenly medium brown. *Pronotum.* Anterior flange narrow, slightly produced dorsad. Posterior flange of females barely covering mesoacrotergite, in males valve-like, overlapping acrotergite until slightly before midpoint of mesoprescutum, margin with small parallel wrinkles oriented toward center point, allowing margin to drape slightly over mesoprescutum, ventral surface with thick coating of white crystalline material. Pronotum coloration in females more or less evenly medium to somewhat dark brown, slightly paler in crevices; in males, pattern as in females except dorsal surface of posterior flange submarginally to nearly completely dark brown, margin sometimes paler, dark surfaces velvety. In females, all surfaces with medium to somewhat long, slender, golden brown to brown setae; males as in females but long setae becoming somewhat sparse on mesodorsal surface of valve. *Pteronotum*. More or less evenly brown to dark brown; velvety spots of metascutum only slightly darker than other surfaces of sclerite; entire surface of pteronotum covered with moderately dense, moderately long, slender, golden brown setae. *Pleuron* base color brown, a pair of broad oblique yellow stripes descending from wing bases to venter; pleural setae moderately dense, moderately long, very fine, very pale yellow, appearing somewhat more conspicuous on stripes, stripes often with a light dusting of pruinescence.

Legs. Femora and tibiae mostly pale yellow, anterolateral surfaces of first two legs dusky medium brown; tarsi very dark brown to black, distal two-fifths of terminal tarsomere diffusely reddish. Coxae setae very pale yellow; antennal comb setae slightly elongate, predominately golden, a few black ones distally.

Wings. Dimension and shape. Long, moderately narrow, apically acute. FW very subtly falcate. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with five to six forked and unforked dull yellow to brown veinlets; membrane usually pale yellow, sometimes faintly tinted with brown, translucent to somewhat opaque, distal margin of pigment straight to weakly crescent shaped, slightly produced along margin and with a small portion of pigment produced along Sc + R one cell width. Deltus predominately dark brown, especially anteriorly, narrowly paler posterodistally. Presectoral area with ten to twelve cells. Rs with six to seven forks. $Mp_2 + Cua_1$ somewhat steeply curving toward hind margin in distal portion. Cubital area with ca. nine to twelve irregular but more or less complete rows of cells. Cubital triangle distal domain with three to four cells. Anal area hind margin convex, anal angle not developed into a process, a single cell row distad of Cup + 1a, with ca. two to five cells in distal half divided by crossveins. *Color and patterning.* Venation medium to dark brown. Costal and subcostal areas fuscous, pigment sometimes narrowly absent in marginal portions of costal cells near wing base. Presectoral area with veinlets often thinly anterolaterally margined, this sometimes continuing to anterolateral veinlets of cell subtending R in radial area. Apical one-fifth of wing fuscous, proximal margin of pigment very diffuse, pigment sometimes reduced to only fill apical area, sometimes faint. HW. As in forewing except as follows. Mp_2 fork angle ca. 65°. Medial triangle distal domain conspicuously long with two to five narrow and elongate cells. Pre-Cup axillary disk dark brown in anterior portion, transitioning to yellow in posterior portion. Pre-Mp_1 area margin not expanded. Anal area with three more or less complete rows of cells.

Abdomen. In males reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. More or less evenly brown; T1 and proximal portions of T2 with moderately dense, moderately long, wispy, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly brown, S1 to S3 often diffusely yellow, other sternites sometimes with diffuse yellowing; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Brown, in females with some irregular yellow mottling, devoid of long setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible. *Macerated specimens.* S9 apical margin obtusely angled. Pulvini very reduced, poorly formed, hardly longer than broad, bearing numerous moderately short, slender, brown setae, but only at apex. GPC weakly sclerotized; in lateral view dorsal margin weakly arched in basal half, mesally shallowly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view moderately broad laterally. Parameres in ventral view with proximal margins weakly differentiated. Pelta moderately sclerotized, broadly almond-shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae and distivalvae pale yellowish brown to dark brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. three times width. Linguella somewhat developed but weakly sclerotized, bearing several short, stiff, slender, setae. Interdental space more or less round. Interdens moderately well sclerotized, small, with a round base, short, cylindrical, nipple- or pin-like, bearing at least one short, slender, seta.

Variation. One specimen with anterosagittal plate pale brown (JRJ_00588).

Type material examined.—*Holotype* (A3 Fig. 58), **new designation**, male, Brazil, in CUAC collection: "COSTA RICA: Limon Rio Uatsi, ca. 8 km (air) W Bribri 9.62 N, 82.90 W 25.iii.1987, el 60 m Holzenthal, Hamilton, Heyn /// Haploglenius luteus det. Penny, 92 /// HOLOTYPE Haploglenius procerus Jones ♂ design. J. R. Jones 2014 /// JRJ_00585". Condition: excellent; antennae and wings spread, left middle leg tarsus missing.

Additional material examined.—*Costa Rica*: Heredia (UDCC: 1 ♂, JRJ_00586). *Honduras*: Atlantida (FSCA: 1 ♂, JRJ_00334); Olancho (FSCA: 1 ♀, JRJ_00595). *Panama*: Colon (SDMC: 1 ♀, JRJ_00594; SEMC: 1 ♂, JRJ_00591; TAMU: 2 ♀♀, JRJ_00587, JRJ_00593); Panama (BYUC: 1 ♂, JRJ_00588; FSCA: 2 ♂♂, JRJ_00419, JRJ_00589; EMUS: 1 ♂, JRJ_00590; SDMC: 1 ♂, JRJ_00592; UCDC: 1 ♂, JRJ_00353).

Morphology, biology and ecology.—Several specimens were collected at UV lights.

Discussion.—This species, which exhibits several of the diagnostic features of *Haploglenius* (thoracic pleuron with paired pale stripes, HW anal area with three complete rows of cells), also expresses strong similarities with *Ascalobyas*: the FW anal margin is distinctly convex, the FW costal area is infuscate, the wingtips are darkened, and the pterostigmata are yellow. By virtue of these and other shared characteristics, *procerus* was placed at the base of the entire clade of *Haploglenius* species. It also demonstrates several transition features from *Ascalobyas* to *Haploglenius*: its antennae are longer than those of *Ascalobyas* but shorter than most other *Haploglenius*, and the number of cells in the FW presectoral area is variable (rather than rigidly fixed) and increased by only one to three from *Ascalobyas*, but not yet always as many as in some species of *Haploglenius*. *Haploglenius procerus* is truly a transitional species.

It also resembles *Haploglenius peruvianus* (and to a lesser extent *Haploglenius luteus*) in the infuscation of the costal areas, the slight darkening of the wingtips, and wing shape. It may have been confused for all of these species by past authors. One specimen in loan material was labeled as *A. microcerus*; another was labeled as *H. luteus*.

Specimen JRJ_00595 is a large female from Honduras in good condition, with the frons and labrum yellow. The distinctly yellow labrum suggests that this specimen is *luteus*, but the frons is uncharacteristically pale for *luteus* and *brunneus*, and it may simply be an anomalous individual. This specimen is very large and lacks verticils and is not *costatus*. It is tentatively placed within *brunneus* due to its geographic distribution.

Haploglenius peruvianus *van der Weele, 1909*

(A3 Figs. 59–60, 92)

Haploglenius peruvianus van der Weele, 1909

—van der Weele 1909.01.05 r#420: 45, figs. 16, 17 {OD: ♂♀, D, DIS. TS: not indicated [syntypes, 3 ♂♂, 1 ♀; a lectotype is here designated from syntype material—see "Type material examined" below]. TL: "Chanchamayo, Peru". TR: "van der Weele private collection" [BMNH; for other syntypes, RMNH—see Penny 1982b]. Type specimen examined (see "Type material examined" below).}

—Navás 1912b.10.31 r#542: 208 {D, GD, K, SR}

—Navás 1913 r#1207: 47 {D, GD, K, SR}

—Banks 1924.01.?? r#76: 437 {MOR}

—Navás 1929.02.?? r#860: 107, 109 {D, GD, L}

—Shetlar 1977 r#5727: 85, 95 {Ph.D. dissertation, nomenclatural acts invalid: L, MOR}

—Penny 1978.09.15 r#5098: 13 {GD, L}

—Penny 1982b r#5103: 624, fig. 9, map 7 {D, DIS, GD, K, MOR, RD: ♂, SR}

—Penny 2002.10.21 r#10230: 179, fig. 9 {AD, D, FP, GD, HAB, K}

—Ábrahám 2013.04.30 r#?????: 179 {GD, L, TL, TR, TS}

Etymology and nomenclatural notes.—*peruvianus*: peruvianus (Latin), 'Peruvian'. Referring to the collection locality of the syntype specimens, which were all collected in Chanchamayo, Peru.

Diagnosis.—Pterostigma pigment yellow, distal margin of pigment very slightly crescent-shaped. Wing apices sometimes very diffusely infuscate. FW hind margin distad of anal angle convex. FW anal area cell row with cells divided by oblique crossveins. HW anal area with three well-developed rows of cells. Distal domain of medial triangle <2x width at base, comprising two to three not especially narrowed cells. Males: Pronotal valve somewhat well-developed. Acrotergite simple, not bilobed. Pleuritocavae absent.

Autapomorphies.—clypeus without dorsolateral maculation; male HW basiposterior margin somewhat convex after anal angle and not changing angle at Mp_1, but wing somewhat narrow and more strap-like; very small pouch-like pleuritocavae present on segment 8.

Distribution.—Bolivia, Brazil, Ecuador, Peru.

Description.—

Size (mm). Male: length of body 33–34, abdomen 24–25, forewing 34–37, hind wing 30–32, antennae 22–23. Female: length of body 32–35, abdomen 22–24, forewing 42–43, hind wing 36–38, antennae 22.

Head. Breadth at widest point (of eyes) slightly greater than that of mesothorax at wing base. Occiput reddish brown, a large, subtriangular, irregular yellow macula along lateral margin, sometimes additional small diffuse yellow maculations dorsad. Vertex brown; setae moderately dense, moderately long, dark brown near antennae, transitioning to mixed golden and dark brown dorsad and dark brown posteriorly. Extra-torular sclerites medium to dark brown. Paraocular band dark brown near antennae, becoming yellow laterad of ventral portion of frons and clypeus, and along orbital sclerite. Frons dusky dark brown dorsolaterally, dusky yellow or orangish mesoventrally; setae moderately dense, golden brown with dark brown tips. Clypeus yellow. Labrum concolorous with mesal portion of clypeus, occasionally slightly darker, sometimes sagittally with a diffuse, narrow, reddish brown stripe. Mandibles dull yellow basally, transitioning to very dark reddish brown apically. Labium pale yellow, with a thin dark brown sagittal line. Eyes very slightly dorsoventrally oblong but symmetrical, with only a very faint mesal flattening. Antennae flagellomeres very weakly swollen at nodes, flagellum pale yellowish or reddish brown, nodes very pale to yellow; clubs elongate pyriform, dark brown, anteriorly yellowish, yellow region divided by a diffuse sagittal brown stripe, covered in fine dark setae; verticils absent.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite dark brown, becoming yellow at base. *Pronotum.* Anterior flange narrow, slightly produced dorsad. Posterior flange of females covering mesoacrotergite, in males valve-like, overlapping acrotergite to midpoint of anterior swelling of mesoprescutum, ventral surface often with coating of white crystalline material. Pronotum coloration in females more or less evenly brown, bearing yellowish sublateral maculations on anterior flange and posterior flange; in males, pattern as in females except posterior flange base color dark brown and margin often paler to reddish, and sublateral yellow maculations sometimes absent. All surfaces with medium to somewhat long, slender, yellow to golden brown setae. *Pteronotum*. Somewhat dark earthy brown, lateral surfaces of mesoprescutum yellow, paler or yellowish areas sometimes present on tegular surface of mesoscutum, anterior surface of mesoscutellum, and on anteromesal and anterolateral surfaces of posterior swelling of mesoscutellum; velvety spots of metascutum dark brown; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color brown, a pair of oblique pale yellow stripes descending from wing bases to venter; pleural setae moderately dense, moderately long, very fine, very pale yellow and golden, stripes often with a light dusting of pruinescence.

Legs. Femora and tibiae mostly pale yellow, anterolateral surfaces of first two legs dusky medium to dark brown; tarsi very dark brown to black, distal two-fifths of terminal tarsomere diffusely reddish. Coxae setae very pale yellow; antennal comb setae predominately golden yellow, becoming black along anterior margin.

Wings. Dimension and shape. Long, moderately narrow, apex posteriorly acute. FW very subtly falcate. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with five to six forked and unforked yellow to brown veinlets; membrane usually pale yellow, sometimes faintly tinted with brown, translucent to somewhat opaque, distal margin of pigment weakly crescent shaped, slightly produced along margin and with a small portion of pigment produced along Sc + R one cell width. Deltus brown, darkening anteromesally. Presectoral area with eight to eleven, usually ten or eleven, cells. Rs with five to six forks. Mp_2 + Cua_1 evenly to somewhat flatly curving toward hind margin in distal portion. Cubital area with ca. nine to twelve irregular but more or less complete rows of cells. Cubital triangle distal domain with three to four cells. Anal area hind margin straight to very weakly convex, anal angle not developed into a process, a single cell row distad of Cup + 1a, with zero to ca. four cells in distal half divided by crossveins. *Color and patterning.* Venation medium to dark brown. Costal and subcostal areas fuscous, pigment sometimes narrowly absent in marginal portions of costal cells near wing base. Presectoral area and proximal portion of radial area sometimes with anterior portions of cells subtending R narrowly tinted brown. Apical one-fourth of wing sometimes weakly fuscous, pigment sometimes reduced to anterior portion of apical area. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90° in males, more acute in females. Medial triangle distal domain only somewhat elongate, with two to three cells. Pre-Cup axillary disk dark brown, surrounding sclerites and membranes often yellowish. Pre-Mp_1 area margin not expanded. Anal area with three more or less complete rows of cells, some crossveins dividing posterior two rows sometimes absent.

Abdomen. In males reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. More or less evenly brown, sometimes distal margin of each tergite with a diffuse, transverse, narrow dark brown band; T1 and proximal portions of T2 with moderately dense, moderately long, wispy, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. Base color brown, but surfaces often mottled with or completely and diffusely yellow, S1 and S2 usually yellow, S2 and often S1 with a narrow dark reddish brown sagittal line; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, often with irregular yellow maculation, this sometimes forming into ca. three or four oblique stripes, devoid of long setae.

Male terminalia. Unmacerated specimens. GPC not everted, pulvini not visible, ectoprocts and S9 dark brown. *Macerated specimens.* S9 apical margin obtusely angled, but angle very sharp, nearly 90°. Pulvini small, weakly sclerotized, length about two times width at base, about one-third length of dorsum of GPC, subapical setae very short, slender, lacking pigment, apical setae moderately short, very slender, pale brown. GPC somewhat sclerotized; in lateral view dorsal margin weakly arched in basal half, mesally shallowly and broadly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view moderately broad laterally, lateral margin distinctly convergent apicad. Parameres in ventral view with truncated or angled apices, proximal margins weakly differentiated. Pelta well sclerotized, elongate ovoid, with numerous minute pores.

Female terminalia. Unmacerated specimens. Ventrovalvae brown to dark brown, distivalvae yellow to brown, ectoprocts brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. three times width. Linguella somewhat well developed but weakly sclerotized, bearing several short, stiff, slender, setae. Interdental space more or less round or weakly diamond-shaped. Interdens sclerotized, with a round base, short, cylindrical, cone-like.

Variation. In specimen JRJ_00654, only two cells divided by crossveins in posterior cell row of HW anal area.

Variation.—An anomalous female (JRJ_00654) from Brazil has just two complete rows of cells in the anal area of the HW, with a few cells in the posterior row divided by crossveins.

Type material examined.—*Lectotype*, **new designation**, male, Brazil, in BMNH collection: “Chanchamayo Peru 1903 /// Coll. ROSENBERG Acq. 1903. /// 1916-240 /// Paratype /// Haploglenius peruvianus type Vd Weele /// LECTOTYPE Haploglenius peruvianus van der Weele ♂ design. J. R. Jones 2014 /// JRJ_01642”. Condition: good; antennae and wings spread, right antennae attached with glue, left antennae, left front leg, left middle leg, and abdomeinal segments 8+ missing.

Additional material examined.—*Brazil*: Amazonas (INPA: 1 ♂, JRJ_00624); Rondônia (CLEV: 1 ♀, JRJ_00654). *Bolivia*: Cochabamba Dept (FSCA: 2 ♂♂, JRJ_00626, JRJ_00627). *Ecuador*: Napo (CAS: 1 ♂, JRJ_00623 [A3 Fig. 59]; EMUS: 1 ♀, JRJ_00625); locality uncertain (MFNB: 1 ♂, JRJ_00598). *Peru*: San Martin (BMNH: 1 ♀, JRJ_01636 [A3 Fig. 60]).

Morphology, biology and ecology.—Collection labels report specimens collected at MV and "mist lights", and at elevations from 200 to 400 m.

Discussion.—Van der Weele indicated that he examined 3 males and one female from Chanchamayo Peru, and that these were retained in his personal collection. Penny (1982b) reported that they are now in the RMNH collection, but one male was discovered at the BMNH and was borrowed for this study. It is in reasonably good condition (unfortunately the very tip of the abdomen is missing, but the identification is unmistakable) and is selected as the lectotype.

This species is rather similar to the new species *Haploglenius procerus*, but has smaller males, reduced darkening of the wing apices, and hind wings with the base narrower. As evidenced by specimen JRJ_00654, the third row of cells in the anal area of the HW is often, but not always fully developed, providing a clue to its transitional position within the phylogeny of NWH near the base of the *Haploglenius* clade. Van der Weele (1909) also considered this a transitional form between *Haploglenius* and *Byas*.

Haploglenius costatus *(Burmeister, 1839)*

(A3 Figs. 61–62, 92)

Ascalaphus costatus Burmeister, 1839

—Burmeister 1839 r#1771: 1000 {OD: sex not indicated. TS: lectotype and paralectotypes designated by Ábrahám 2013 from syntype material). TL: "Bahia" (Brazil). TR: "v. Winthems Sammlung" (ZMH—see van der Weele 1909, Penny 1982b, Ábrahám 2013). Type specimen not examined (see "Discussion" below).}

—Lefèbvre 1842.04.?? r#3666: 6 {TSP (of *Ptynx* new genus; =misidentification of *Ascalaphus appendiculatus* Fabricius; see "*Type species of Ptynx Lefèbvre, Neuroptynx McClendon and Ascaloptynx Banks*" under "Discussion" below)}

—Hagen 1861.07.?? r#455: 327 {DIS, GS, L, SYN}

—Hagen 1866 r#460: 382 {L, SYN}

—Orfila 1949 1949 r#5020: 189, 190 {DIS, MOR, TSP (of *Haploglenius* Burmeister)}

—Oswald and Penny 1991.12.02 r#7138: 28 {TSP (of *Haploglenius* Burmeister, 1839, *Ptynx* Lefèbvre, 1842, and *Neuroptynx* McClendon, 1906 [the latter two type assignments involve a misidentification of *Ascalaphus appendiculatus* Fabricius; see "*Type species of Ptynx Lefèbvre, Neuroptynx McClendon and Ascaloptynx Banks*" under "Discussion" below])}

—Ábrahám 2013.04.30 r#?????: 174 {SYN}

Ptynx costata (Burmeister, 1839) *sensu* Lefèbvre not Burmeister

—Lefèbvre 1842.04.?? r#3666: 6 {NC (=misidentification of *Ascalaphus appendiculatus* Fabricius; see "*Type species of Ptynx Lefèbvre, Neuroptynx McClendon and Ascaloptynx Banks*" under "Discussion" below)}

—McLachlan 1871.09.14 r#353: 239 {SYN}

—Orfila 1949 1949 r#5020: 190 {DIS}

—Shetlar 1977 r#5727: 99 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus appendiculatus* Fabricius)}

Ptynx costata (Burmeister, 1839)

—Hagen 1866 r#460: 459 {L, SYN}

—Ábrahám 2013.04.30 r#?????: 174 {SYN}

Haploglenius costatus (Burmeister, 1839)

—Hagen 1866 r#460: 406 {GD, NC, SYN}

—McLachlan 1871.09.14 r#353: 234, 235, 236 {GD, RD: ♂♀, SYN, TR, TS}

—Taschenberg 1879 r#5954: 218 {D, GD, SR}

—Gerstaecker 1885 r#2556: 2 {MOR}

—van der Weele 1909.01.05 r#420: 56, figs. 22, 23, 24 {DIS, GD, RD: ♂♀, SR, SYN, TR, TS, TL}

—Navás 1912b.10.31 r#542: 208 {D, GD, K, SR}

—Navás 1913 r#1207: 48 {D, GD, K, SR}

—Navás 1919 r#697: 288 {L, GD}

—Navás 1929.02.?? r#860: 109 {D, GD}

—Williner 1945 r#6292: 426 {GD, SR}

—Shetlar 1977 r#5727: 85, 90 {Ph.D. dissertation, nomenclatural acts invalid: L, SYN}

—Penny 1978.09.15 r#5098: 13 {GD, L}

—Penny 1982a r#5105: 398 {TSP (of *Haploglenius* Burmeister; error: should be *Ascalaphus costatus* Burmeister—Arts. 11.9.3.6, 53.3.3)}

—Penny 1982b r#5103: 622, fig. 8, map 6 {BIO, D, FP, GD, HAB, MOR, RD: ♂♀, SR, SYN, TR, TS}

—Tjeder 1992 r#7246: 36 {MOR}

—Penny 2002.10.21 r#10230: 179 {D, MOR}

—Ardila and Jones 2012.04.13 r#14570: 40 {GD}

—Ábrahám 2013.04.30 r#?????: 174, 175, fig. 1 {DIS, GD, SYN, TL, TR, TS}

Ascalaphus luteus Walker, 1853 (part)

—McLachlan 1871.09.14 r#353: 234 {SYN}

Haplogenius [sic] *costatus* (Burmeister, 1839)

—Williner 1945 r#6292: fig. 1 {ISS}

—Penny 1978.09.15 r#5098: 12 {SYN}

Ascalaphus imperator Hagen, 1861

—Hagen 1861.07.?? r#455: 327 {invalid: NNU}

—Ábrahám 2013.04.30 r#?????: 174 {SYN}

Etymology and nomenclatural notes.—*costatus*: costatus (Latin), 'ribbed'. Perhaps referring to the stripes of the thoracic pleuron, which were mentioned by Burmeister in his very brief description.

Diagnosis.—Frons yellow to dull brownish, more or less concolorous with clypeus. Antennae with several verticils near base. Subcostal area undulations only rarely diffusely darkened. Pterostigma veins yellow to brown and pigment dull yellow. FW costal area with distal cells undivided by crossveins. FW anal angle slightly produced, hind margin distad of angle concave. Anal are cell row undivided by crossveins. Males: Pronotal valve well-developed. Acrotergite simple, not bilobed. Pleuritocavae absent.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Argentina, Brazil, (Bolivia, Colombia, Panama?).

Description.—

Size (mm). Male: length of body 34–37, abdomen 22–29, forewing 37–47, hind wing 34–42, antennae 24–30. Female: length of body 27–36, abdomen 18–26, forewing 39–50, hind wing 35–47, antennae 25–29.

Head. Occiput base color reddish brown, pattern often obscured but consisting of irregular diffuse yellow blotches positioned laterally. Vertex sandy brown, sometimes very slightly reddish, yellowish, or darker; setae somewhat dense and dark brown on anterior surface, becoming more sparse and mixed brown and golden brown dorsally and posteriorly, moderately long, slender. Extra-torular sclerites concolorous with frons. Paraocular band dark brown near antennae and often bordering frons, becoming yellow along orbital sclerite and ventrolaterally near margin of frons and clypeus. Frons dusky yellow to orange, sometimes slightly paler or darker, occasionally a diffuse and incomplete reddish brown sagittal line present; setae moderately dense, mixed dark brown to black and golden yellow. Clypeus yellow, often laterally diffusely reddish brown, this color sometimes concentrated into a somewhat distinct maculation. Labrum concolorous with mesal portion of clypeus, sometimes with a diffuse brown dorsal or mesal sagittal maculation. Mandibles dull yellow basally, transitioning to very dark reddish brown apically. Labium pale yellow, with a thin dark brown sagittal line. Eyes very slightly dorsoventrally oblong, slightly larger in ventral half, with only a very faint mesal flattening. Antennae flagellomeres very weakly swollen at nodes, flagellum pale yellowish or reddish brown, nodes paler, verticils present on basal flagellomeres directed anterad, more or less coequal in length to a single flagellomere, absent on posterior face;

clubs narrow elongate pyriform, apices acuminate, pale brown to yellow, anterior face divided by a narrow diffuse longitudinal brown line, covered in fine dark setae.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite dull dark yellowish brown to dark brown, slightly paler ventrally, becoming yellow toward base. *Pronotum.* Anterior flange narrow, slightly produced dorsad. Posterior flange of females covering mesacrotergite, in males valve-like, overlapping acrotergite nearly to midpoint of anterior swelling of mesoprescutum, ventral surface often with a dense coating of white crystalline material. Pronotum coloration variable, base color dark brown, anterior flange sometimes laterally pale brown, medial transverse band sometimes mesally reddish or pale brown, posterior flange dark brown, often velvety, laterally diffusely pale brown or yellowish. All surfaces with medium to somewhat long, fine, brown to golden brown setae. *Pteronotum.* In males, distal margin of mesacrotergite not produced posterad, weakly flange-like laterally, not bilobed, entire. Dorsal surface of pteronotum proper mostly evenly medium to dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum diffusely yellow and occasionally anterior faces and mesal portion of posterior swelling of mesoscutellum paler; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, brown to golden brown setae. *Pleuron* base color brown, a pair of oblique yellow stripes descending from wing bases to venter; pleural setae moderately dense, moderately long, fine, mixed golden brown and brown, stripes sometimes with a light dusting of pruinescence.

Legs. Femora and tibiae pale brown or orangish to yellow, mesal surfaces of femora of first two legs often brown to dark brown; tarsi reddish brown, proximal margins dark brown and tarsi appearing annulated. Coxae setae very pale yellow; antennal comb setae predominately golden yellow.

Wings. Dimension and shape. Long, moderately narrow, apex posteriorly weakly acute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with four to five forked and unforked pale yellow to brown veinlets; membrane usually pale yellow, sometimes faintly tinted with brown, translucent to somewhat opaque, distal margin of pigment long and straight. Deltus brown, sometimes darkening anteromesally, usually translucent. Presectoral area with ca. eleven to fifteen cells. Rs with five to six forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine to eleven irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin somewhat concave, anal angle weakly developed into a process, not yet tooth-like, a single cell row distad of Cup + 1a, cells usually undivided by crossveins. *Color and patterning.* Venation pale to dark brown. Costal and subcostal areas fuscous, sometimes weakly, pigment very narrowly absent along anterior margin of costal cells; subcostal area usually without pseudoveinlets, sometimes anterior portions of undulations very weakly pigmented. Presectoral area usually with anterior portions of cells subtending R narrowly tinted brown. Apex of wing sometimes very weakly fuscous, darkening often reduced to anterior portion of apical area. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain rather short with one to two cells, shorter and often reduced to a single cell in females. Pre-Cup axillary disk yellow, anterior margin narrowly brown. Pre-Mp_1 area margin very slightly expanded, if at all. Anal area with three complete rows of cells, sometimes one or two crossveins dividing posterior two rows absent.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly brown; T1 and T2 with moderately dense, moderately long, wispy, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. S1 and S2 yellow with a narrow dark brown sagittal line, S3 and portions of S4 often diffusely yellow, remainder of sternum more or less evenly medium to dark brown; mostly devoid of long setae, some moderately long, wispy, pale golden setae on S1 and S2. *Pleural membrane*. Dark brown, often with ca. three or four irregular yellow maculations, these sometimes forming into oblique stripes, devoid of long setae.

Male terminalia. Unmacerated specimens. Pleuritocavae not visible, GPC not everted, pulvini not visible, ectoprocts and S9 brown, distal margins sometimes thinly paler yellow. *Macerated specimens.* S9 apical margin obtusely angled, but angle very shallow, nearly straight. Pulvini very small, unsclerotized, weakly differentiated from gonosaccal membrane, with a few moderately long, slender, subapical setae, and at least one very long, more robust but still rather slender apical seta, all setae brown. GPC somewhat sclerotized; in lateral view dorsal margin weakly arched in basal half, mesally broadly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view moderately broad laterally. Parameres in ventral view slightly short and broad, proximolateral margins weakly differentiated. Pelta weakly sclerotized, ovoid.

Female terminalia. Unmacerated specimens. Ventrovalvae reddish brown and yellow, distivalvae pale reddish to yellowish brown, ectoprocts reddish brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. three times width. Linguella very slightly produced and bulb-like but poorly sclerotized and weakly differentiated from surrounding membrane, bearing several short, stiff, slender setae. Interdental space more or less round. Interdens sclerotized, with a round base, short, cone-shaped.

Variation. Specimen JRJ_00615, a male from Panama, appears to be a specimen of *costatus* in general habitus and features, for example, overall size, coloration and patterning of body and wings, overall wing shape and venation, and most diagnostically, the presence of verticils and the reddish and darkly annulated color of the tarsi. However it differs in having the pronotal valve completely covering the mesoprescutum, the mesoacrotergite being weakly bilobed, the FW pterostigma membranes being strongly pigmented dark reddish brown and mesally opaque, and in having small pleuritocavae on the distal margin of segment 7. Being located so far from the center of distribution of most other individuals examined in this study, this specimen may simply be a geographical variant, or it may in fact represent an altogether different species, but more specimens are required to determine this. A single other male from Colombia (JRJ_00465) also has the longer pronotal valve and small pleuritocavae, but the FW pterostigmata membranes are translucent and only very slightly tinged with brown, and the mesoacrotergite does not appear to be bilobed. A single female from Colombia may be allied to the male; it differs from other females of *costatus* in having the HW apices distinctly fuscous in apical one-fifth, as in some *brunneus* females; the FW apical area is also diffusely fuscous. Its pterostigmata do not differ from those of the male. The Panamanian and Colombian specimens all have the distal margin of the labrum at least tinged reddish brown to brown; they may even represent anomalous individuals of *brunneus* with the labrum only partially darkened and verticils present. Specimen JRJ_00501, a female from Bolivia, also occurs far west of the main body of the specimens examined in this study; in this and a few other similar specimens from the same area, the disgnostic features of FW anal margin shape and the presence of verticils are expressed, but the pterostigma membranes are evenly translucent brown and the anterior portion of the apical area is narrowly tinged with brown color; the setae of the ventrovalvae are somewhat broader and the linguella setae are small and very fine and thus less robust. As with the previous specimen, this individual and a few others like it from Bolivia may represent geographical deviation or a different species altogether, but more specimens are required to make this determination.

Type material examined.—Not available for this study.

Additional material examined.—*Argentina*: Misiones (SDMC: 14 ♂♂, JRJ_00561, JRJ_00562, JRJ_00563, JRJ_00564, JRJ_00565, JRJ_00566, JRJ_00567, JRJ_00568,

JRJ_00569, JRJ_00570, JRJ_00571, JRJ_00572, JRJ_00573, JRJ_00575, 3 ♀♀, JRJ_00550, JRJ_00557, JRJ_00560). *Bolivia*: Beni Dept (MFNB: 1 ♀, JRJ_01779); La Paz Dept (EMUS: 2 ♀♀, JRJ_00501, JRJ_00502; USNM: 1 ♀, JRJ_00503). *Brazil*: Bahia (INPA: 3 ♀♀, 00539, JRJ_00540, JRJ_00548; MFNB: 1 ♂, JRJ_01760, 2 ♀♀, JRJ_01759, JRJ_01782; NMW: 1 ♂, JRJ_00517 [A3 Fig. 61], 3 ♀♀, JRJ_00535, JRJ_00537, JRJ_00538); Espirito Santo (MFNB: 1 ♂, JRJ_01767; SDEI: 1 ♂, JRJ_01502); Federal (MSUC: 1 ♂, JRJ_00514); Minas Gerais (FSCA: 1 ♂, JRJ_00513; INPA: 1 ♂, JRJ_00527); Para (MFNB: 1 ♀, JRJ_00529); Paraná (INPA: 2 ♂♂, JRJ_00496, JRJ_00497, 1 ♀, JRJ_00451; TAMU: 1 ♀, JRJ_00453; UMSP: 1 ♀, JRJ_00456); Rio de Janeiro (DEBU: 1 ♂, JRJ_00515; MFNB: 2 ♂♂, JRJ_01763, JRJ_01768, 1 ♀, JRJ_01765); Rio Grande do Sul (INPA: 1 ♀, JRJ_00531; MFNB: 1 ♂, JRJ_01766; NMW: 1 ♂, JRJ_00516; SDEI: 1 ♂, JRJ_01500); Santa Catarina (INPA: 3 ♂♂, JRJ_00519, JRJ_00520, JRJ_00521, 4 ♀♀, JRJ_00532, JRJ_00533, JRJ_00542, JRJ_00547; NMW: 2 ♂♂, JRJ_00524, JRJ_00525, 1 ♀, JRJ_00534 [A3 Fig. 62]; SDMC: 1 ♂, JRJ_00509; TAMU: 4 ♂♂, JRJ_00508, JRJ_00510, JRJ_005115, JRJ_00512, 2 ♀♀, JRJ_00543, JRJ_00544); São Paulo (EMEC: 1 ♀, JRJ_00530; EMUS: 1 ♀, JRJ_00541; SDEI: 1 ♂, JRJ_01749; UMSP: 1 ♀, JRJ_00546); locality uncertain (MFNB: 1 ♀, JRJ_01762; MHNG: 2 ♂♂, JRJ_00504, JRJ_00505; NMW: 1 ♀♀, JRJ_00536). *Colombia*: Magdelena (CMNH: 1 ♂, JRJ_00465, 1 ♀, JRJ_00500). *Ecuador*: locality uncertain (MFNB: 2 ♂♂, JRJ_01774, JRJ_01783). *Panama*: Panama (FSCA: 1 ♂, JRJ_00615). *Peru*: locality uncertain (MFNB: 1 ♀, JRJ_01764). *"South America"*: (MFNB: 1 ♂, JRJ_01756). *Country unknown*: (MFNB: 1 ♀, JRJ_01761;

SDEI: 3 ♂♂, JRJ_01503, JRJ_01504, JRJ_01748; UNESP: 1 ♀, JRJ_00578; USNM: 1 ♂, JRJ_00579, 1 ♀, JRJ_00580).

Morphology, biology and ecology.—Labels on loan material report specimens being collected at lights and light sheets, and at elevations ranging from 300 to 900 m.

Discussion.—*Haploglenius costatus* is a common species widespread in southeastern Brazil. It was one of the first species described in the subfamily and, with *luteus*, expresses a somewhat plesiomorphic phenotype (posterior margin of the FW anal area slightly concave) intermediate between the basal-most species (*procerus*, *peruvianus*), which have a convex posterior margin in the FW anal area, and the remaining *Haploglenius* species, which have the posterior margin in the FW anal area slightly to considerably concave and express numerous derived features that set them apart. In fact, *costatus* and *luteus* are somewhat variable in size and wing venation and are often confused for one another. They can usually be easily separated, however—*costatus* males have a smaller and narrower pronotal valve, the mesoacrotergite is entire and not bilobed, and the pleuritocavae are essentially absent. Specimens of both sexes of *costatus* are often very slightly smaller than those of *luteus*, and *costatus* expresses another unique feature not yet reported: basal verticils on the antennae. They are not as numerous as those of gerstaeckeri, but they occur consistently. A very few specimens of *luteus* from the northern part of its range have also been observed to express a few verticils. For the most part, the distributions of the two species also appear to not overlap.

The largest numbers of specimens in loan material were collected from areas centering around southeast Brazil. A few geographic outliers, however, were discovered, and it is not yet exactly clear if they are truly specimens of *costatus*, or if they represent outshoots with very similar morphotypes. One small group of females are from Bolivia; a female and two males are from Colombia and Panama; all have dark pterostigmata veins, different from most specimens of *costatus* in which the veins are pale yellowish. The female from Colombia has HW apex broadly darkened and FW narrowly and slightly darkened; the male from Panama has very dark FW pterostigmata (see also 'Variation' above).

A specimen identified by Tjeder (1992: 36 fig. 90) as *costatus* is almost certainly *luteus* or *brunneus*, based on the emarginated posterior margin of the acrotergite.

Haploglenius normani ***new species***

(A3 Figs. 63, 93)

Etymology and nomenclatural notes.—*normani;* a Latinized noun. Named in honor of Norman Penny, a great neuropterologist who has devoted much of his research to the taxonomy of New World owlflies.

Diagnosis.—Smaller than *costatus*. Antennae with several verticils near base. Tarsi pale reddish brown. Acrotergite simple, not bilobed. FW costal area with distal cells undivided by crossveins. Pterostigma veins dark brown and pigment pale to dark brown. Apical area without pigment. Cell row subtending R not infuscated. FW anal angle slightly produced, hind margin distad of angle concave. FW anal area cell row undivided by crossveins. HW anal area with two rows of cells. Males: Pronotal valve slightly developed, articulable. Pleuritocavae absent.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Argentina, Bolivia, Brazil, Peru.

Description.—

Size (mm). Male: length of body 26–36, abdomen 16–25, forewing 33–37, hind wing 27–31, antennae 22–23. Female: length of body 23–33, abdomen 16–23, forewing 39–43, hind wing 33–36, antennae 22–24.

Head. Slightly smaller than in other species, breadth at widest point (of eyes) narrower than that of mesothorax at wing base. Occiput base color reddish brown, pattern often obscured but consisting of irregular diffuse yellow blotches positioned laterally. Vertex sandy reddish brown, darker brown laterally, often paler or orangish anteriorly; setae variably dense, sometimes rather sparse, usually denser and mixed dark brown and gold on anterior surface, becoming more sparse dorsally and posteriorly, moderately long, slender. Extra-torular sclerites concolorous with dorsolateral portions of frons. Paraocular band dark brown near antennae and often bordering frons, becoming yellow along orbital sclerite and ventrolaterally near margin of frons and clypeus. Frons dusky yellow to orange, becoming dusky brown dorsolaterally, occasionally a diffuse and incomplete reddish brown sagittal line present; setae moderately dense, dark brown. Clypeus yellow, often laterally diffusely reddish brown, this color sometimes concentrated into a somewhat distinct maculation. Labrum concolorous with mesal portion of clypeus. Mandibles dull yellow basally, transitioning to very dark reddish brown apically. Labium pale yellow, with a thin dark brown sagittal line. Eyes very slightly dorsoventrally oblong, slightly larger in ventral half, with weak posteromesal flattening. Antennae flagellomeres weakly swollen at nodes, flagellum pale yellowish or reddish to medium dark brown, nodes usually paler, verticils present on basal flagellomeres directed anterad, more or less coequal in length to a single flagellomere, absent on posterior face; clubs narrow elongate pyriform, apices weakly acuminate, color variable, in many females completely yellow, otherwise yellow posteriorly, anterior face divided by and often nearly completely covered with a broad longitudinal brown stripe, covered in fine golden brown setae.

Thorax. Cervix. Dorsal cervical plate setae golden yellow. Cervical sclerite dark brown, narrowly yellow toward base. *Pronotum.* Anterior flange a narrow collar, mesally slightly broader, very weakly produced dorsad sublaterally, slightly bilobed. Posterior flange of females barely covering mesacrotergite, in males valve-like, overlapping acrotergite and anterior portion of anterior swelling of mesoprescutum, ventral surface often with a dense coating of white crystalline material. Pronotum coloration variable, base color dark brown, anterior flange sometimes laterally pale brown or orange, medial transverse band sometimes mesally with small irregular yellow to red maculations, posterior flange dark reddish brown, laterally often diffusely pale brown or yellowish. All surfaces with medium to somewhat long, fine, brown to golden brown setae. *Pteronotum*. In males, distal margin of mesacrotergite not produced posterad. Dorsal surface of pteronotum proper mostly evenly medium to dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum diffusely yellow; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, brown to golden brown setae. *Pleuron* base color dark brown, a pair of oblique yellow stripes descending from wing bases to venter; pleural setae moderately dense, moderately long, fine, brown on mesanepisternum, otherwise very pale yellow, stripes sometimes with a light dusting of pruinescence.

Legs. Femora and tibiae base color yellow, pro- and mesothoracic femora mesally to completely dark dusky brown, anterolateral faces of tibiae also dusky dark brown, distal third of femur and proximal third of tibia on anterolateral surfaces of metathoracic leg often slightly darker; tarsi pale reddish brown, proximal margins dark brown and tarsi appearing annulated. Coxae setae very pale yellow or white; antennal comb setae golden.

Wings. Dimension and shape. Long, moderately narrow, apex posteriorly weakly acute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with four to six forked and unforked pale brown veinlets, these often margined with dark brown pigment; membrane pale to dark brown, translucent to somewhat opaque, distal margin of pigment long and straight. Deltus brown, often darkening anteromesally, sometimes translucent, often becoming opaque at least anteriorly. Presectoral area with ca. nine to twelve cells. Rs with ca. six forks. Mp_2 + Cua_1 evenly to somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine to eleven irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin weakly concave, anal angle weakly developed into a process, not yet tooth-like, a single cell row distad of Cup + 1a, cells undivided by crossveins. *Color and patterning.* Venation pale to dark brown. Costal and subcostal areas fuscous, sometimes weakly, pigment very narrowly absent along anterior margin of costal cells; subcostal area without pseudoveinlets. Presectoral area sometimes with anterior portions of basal cells subtending R narrowly tinted brown. Apex of wing occasionally very weakly fuscous. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain rather short with one to two cells, shorter and often reduced to a single cell in females. Pre-Cup axillary disk yellow. Pre-Mp_1 area margin not expanded. Anal area with two complete rows of cells, posterior row sometimes with a few cells divided by crossveins.

Abdomen. In males usually reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly brown; T1 and T2 with moderately dense, moderately long, wispy, pale golden brown setae, remainder of tergum devoid of long setae. *Sternum*. Base color brown, ventral surfaces of sternites often very diffusely and irregularly pale or yellowish, more often on S1 to proximal portions of S3; mostly devoid of long setae, some moderately long, wispy, pale golden brown setae on S1 and S2. *Pleural membrane*. Dark brown, often with ca. three or four irregular yellow maculations, these sometimes forming into oblique stripes, devoid of long setae.

Male terminalia. Unmacerated specimens. GPC sometimes everted, pulvini not visible, ectoprocts and S9 reddish brown. *Macerated specimens.* S9 apical margin obtusely angled, but angle very shallow, nearly straight. Pulvini extremely reduced, essentially indistinguishable from gonosaccal membrane, only evidenced by a few short, slender, very pale setae. GPC somewhat sclerotized; in lateral view dorsal margin weakly arched in basal half, mesally very weakly notched, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view moderately broad laterally. Parameres in ventral view slightly short, proximolateral margins weakly differentiated. Pelta weakly sclerotized, ovoid.

Female terminalia. Unmacerated specimens. Ventrovalvae pale reddish to dark brown, distivalvae yellowish to reddish brown, ectoprocts reddish to dark brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. two times width. Linguella weakly differentiated from surrounding membrane, bearing several short, stiff, very slender, pale setae. Interdental space more or less round. Interdens sclerotized, short, pin-like.

Variation. Specimen JRJ_00903 with abdominal tergites pale reddish brown, dissected by a narrow brown sagittal line running the length of tergum, and the posterior margin of each tergite and sternite with a diffuse transverse brown band, and sternites otherwise yellowish. This coloration is somewhat distinctive, but the specimen appears to be teneral.

Type material examined.—*Holotype*, **new designation**, male, Peru, in BMNH collection: “Satipo Junín Peru alt. 650m V. 1986 /// W. R. B. Hynd coll. BMNH (E) 1998-129 /// HOLOTYPE Haploglenius normani Jones ♂ design. J. R. Jones 2014 /// JRJ_01641”. Condition: excellent; antennae and wings spread, right hind leg tarsus missing.

Additional material examined.—*Argentina*: Salta (FSCA: 8 ♀♀, JRJ_00549, JRJ_00551, JRJ_00553, JRJ_00554, JRJ_00555, JRJ_00556, JRJ_00558, JRJ_00559); Tucuman (FSCA: 1 ♂, JRJ_00574, 2 ♀♀, JRJ_00552, JRJ_00916). *Bolivia*: Santa Cruz (CMNH: 1 ♀, JRJ_00904; EMUS: 1 ♀, JRJ_00914; FSCA: 1 ♂, JRJ_00651, 2 ♀♀, JRJ_00652, JRJ_00653; INPA: 1 ♀, JRJ_00915; MFNB: 2 ♂♂, JRJ_00913, JRJ_01632). *Brazil*: Amazonas (INPA: 1 ♂, JRJ_00898); Espirito Santo (FSCA: 1 ♂, JRJ_00903); Mato Grosso (INPA: 1 ♂, JRJ_00902); Para (FSCA: 1 ♂, JRJ_00912; INPA: 3 ♂♂, JRJ_00899, JRJ_00900, JRJ_00901, 2 ♀♀, JRJ_00909, JRJ_00910); Pernambuco (INPA: 1 ♀, JRJ_00907); Rondônia (CAS: 1 ♂, JRJ_00905; FSCA: 1 ♀,

JRJ_00897; INPA: 2 ♀♀, JRJ_00908, JRJ_00911); Tocantins (INPA: 1 ♀, JRJ_00906). *Peru*: Junín (BMNH: 1 ♂, JRJ_01643 [A3 Fig. 63]); Cuzco (USNM: 1 ♀, JRJ_00889).

Morphology, biology and ecology.—Labels of a few specimens indicate they were collected at lights.

Discussion.—When specimens of this species were first being evaluated for this study they were interpreted to be *Neohaploglenius rondonianus* Penny, because certain details in Penny's (1982b) description roughly correspond to features seen in the specimens: antennae length, pronotal valve present, tarsi pale reddish brown, costal areas dark, axillary angle distinct, HW anal area with two cell rows, size of males, and the geographic distribution of the specimens. Ábrahám (2013), however, examined Penny's type and determined it is conspecific with *Verticillecerus gerstaeckeri* van der Weele (see 'Discussion' for *gerstaeckeri*, above), which also has these characteristics (the anal angle is *normani* is not actually very distinct). Penny's allotype and paratypes were not examined for this study.

This species is similar to *costatus* but smaller; it can be easily distinguished by the dark veinlets of the pterostigmata, the less well-developed FW anal angle, and the HW anal area having only two cell rows. It is also similar to *gerstaeckeri*, but it lacks the distinctive wing pattern, and has much less developed verticils. All three of these species are closely related and were placed proximate to one another in the cladistic analysis.

This species is dedicated to N. Penny, a talented neuropterologist and friend.

Haploglenius luteus *(Walker, 1853)*

(A3 Figs. 64–67, 94)

Ascalaphus luteus Walker, 1853

—Walker 1853 r#6194: 450 {OD: sex not indicated (♂—see van der Weele 1909, Penny 1982b), D. TS: not indicated [holotype by explicit monotypy]. TL: indicated as unknown. TR: BMNH. Type specimen examined (see "Type material examined" below).}

—Hagen 1861.07.?? r#455: 327 {JSYN (of *Ascalaphus subcostatus* Burmeister)}

—Hagen 1866 r#460: 385 {JSYN (of *Ascalaphus subcostatus* Burmeister)}

—McLachlan 1871.09.14 r#353: 234 {JSYN (part, of *Ascalaphus costatus* Burmeister)}

—van der Weele 1909.01.05 r#420: 47 {SYN}

—Navás 1923b.11.16 r#737: 16 {MOR}

—Banks 1924.01.?? r#76: 437 {D, SYN}

—Shetlar 1977 r#5727: 90 {Ph.D. dissertation, nomenclatural acts invalid: SYN}

—Penny 1978.09.15 r#5098: 13 {SYN}

—Penny 1982b r#5103: 620 {SYN}

—Ábrahám 2013.04.30 r#?????: 174, 175 {JSYN (part, of *Ascalaphus costatus* Burmeister), SYN}

Haploglenius luteus (Walker, 1853)

—van der Weele 1906 r#404: 226 {MOR, NC, SYN}

—van der Weele 1909.01.05 r#420: 47, figs. 19, 20, 21 {D, GD, MOR, RD: ♂♀, SR, SYN, TL, TR, TS}

—Navás 1912b.10.31 r#542: 208 {D, GD, K, SR}

—Navás 1913 r#1207: 48 {D, GD, K, SR}

—Navás 1929.02.?? r#860: 109 {D, GD}

—Eisner and Adams 1976.04.20 r#2200: 304, figs. 1–3 {BIO, DIS, MOR}

—Shetlar 1977 r#5727: 90, figs. 23a–d, 38 {Ph.D. dissertation, nomenclatural acts invalid: D, DIS, GD, K, RD: ♂♀, SR, SYN, TR, TS}

—Penny 1978.09.15 r#5098: 13 {GD, L, SYN}

—Penny 1982b r#5103: 620, fig. 7, map 5 {D, DIS, FP, GD, HAB, MOR, RD: ♂♀, SR, SYN, TR, TS}

—Tjeder 1992 r#7246: 30, figs. 78–80 {MOR}

—Penny 2002.10.21 r#10230: 179, fig. 7 {AD, D, FP, GD, HAB, K}

—Ardila and Jones 2012.04.13 r#14570: 40 {GD}

—Ábrahám 2013.04.30 r#?????: 175, figs. 2–3 {DIS, GD, SYN, TL, TR, TS}

—Onore et al. 2014.03.30 r#15564: 88, figs. 6-7 {BIO, DIS, MOR}

Ascalaphus circumflexus Walker, 1853

—Walker 1853 r#6194: 451 {OD: sex not indicated (♀—see van der Weele 1909, Penny 1982b), D. TS: not indicated [holotype by explicit monotypy]. TL:

“Santarem, Brazil”. TR: BMNH. Type specimen examined (see “Type material examined” below).}

—Hagen 1861.07.?? r#455: 327 {JSYN (of *Ascalaphus albistigma* Walker)}

—Hagen 1866 r#460: 382 {JSYN (of *Ascalaphus albistigma* Walker)}

—McLachlan 1871.09.14 r#353: 234 {JSYN (of *Ascalaphus costatus* Burmeister)}

—van der Weele 1909.01.05 r#420: 47 {JSYN (of *Ascalaphus luteus* Walker), MOR, TS, TL}

—Shetlar 1977 r#5727: 90 {Ph.D. dissertation, nomenclatural acts invalid: }

—Penny 1978.09.15 r#5098: 13 {JSYN (of *Ascalaphus luteus* Walker)}

—Penny 1982b r#5103: 622 {JSYN (of “*Haploglenius costatus* Burmeister” [should be *Ascalaphus costatus* Burmeister]), TR, TS}

—Ábrahám 2013.04.30 r#?????: 175 {JSYN (of *Ascalaphus luteus* Walker)}

Ascalaphus contrarius Walker, 1853

—Walker 1853 r#6194: 452 {OD: sex not indicated (♀—see van der Weele 1909, Penny 1982b), D. TS: not indicated [holotype by explicit monotypy]. TL: “Pará” (Brazil). TR: BMNH. Type specimen not examined (see “Discussion” below).}

—Hagen 1861.07.?? r#455: 327 {JSYN (of *Ascalaphus costatus* Burmeister)}

—Hagen 1866 r#460: 382 {JSYN (of “*Haploglenius costatus* Burmeister” [should be *Ascalaphus costatus* Burmeister])}

—McLachlan 1871.09.14 r#353: 234 {JSYN (of *Ascalaphus costatus* Burmeister)}

—van der Weele 1909.01.05 r#420: 47 {JSYN (of *Ascalaphus luteus* Walker), MOR, TL, TS}

—Shetlar 1977 r#5727: 90 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus luteus* Walker)}

—Penny 1978.09.15 r#5098: 13 {JSYN (of *Ascalaphus luteus* Walker)}

—Penny 1982b r#5103: 622 {JSYN (of "*Haploglenius costatus* Burmeister" [should be *Ascalaphus costatus* Burmeister]), TR, TS}

Haploglenius costatus (Burmeister, 1839) (part)

—Shetlar 1977 r#5727: 90 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus luteus* Walker)}

Haploglenius pictus Gerstaecker, 1885

—Gerstaecker 1885 r#2556: 2 {OD: indicated as ♂♀ (♀♀—see van der Weele 1906), D. TS: syntypes, sex not indicated [2 ♀♀ (see van der Weele 1906, 1909); a lectotype needs to be designated from syntype material]. TL: "Iquitos et Iurimaguas" (Peru). TR: not indicated (EMAU—see Penny 1982b). Type specimen not examined (see "Discussion" below).}

—van der Weele 1906 r#404: 226 {MOR, TS}

—van der Weele 1909.01.05 r#420: 47 {JSYN (of *Ascalaphus luteus* Walker), MOR, TL, TS}

—Shetlar 1977 r#5727: 90 {Ph.D. dissertation, nomenclatural acts invalid: JSYN (of *Ascalaphus luteus* Walker)}

—Penny 1978.09.15 r#5098: 13 {JSYN (of *Ascalaphus luteus* Walker)}

—Penny 1982b r#5103: 622 {JSYN (of "*Haploglenius costatus* Burmeister" [should be *Ascalaphus costatus* Burmeister]), TR, TS}

—Ábrahám 2013.04.30 r#?????: 175 {JSYN (of *Ascalaphus luteus* Walker)}

Haploglenius eurypterus Navás, 1920

—Navás 1920 r#714: 92, fig. 2 {OD: ♀, D, ET. TS: not indicated [holotype]. TL: "Perú, Río Pacaya, Bajo Ucayali". TR: NAVC. Type specimen not examined (see "Discussion" below).}

—Banks 1924.01.?? r#76: 437 {DIS}

—Penny 1978.09.15 r#5098: 13 {GD, L}

—Montserrat 1985 r#4296: ? {TR}

—Montserrat 1986 r#4301: ? {TR}

—Ábrahám 2013.04.30 r#?????: 175 {JSYN (of *Ascalaphus luteus* Walker), TR}

Etymology and nomenclatural notes.—*luteus*: luteus (Latin), 'yellow'. This name could refer to the yellow color of the pleural stripes, some of the sclerites of the face, or the pterostigmata.

Diagnosis.—Frons distinctly darker than clypeus, reddish or smoky amber brown. Labrum yellow. Antennae reddish basally, without verticils. Subcostal area with undulations sometimes darkened to form pseudoveinlets. FW anal area cell row sometimes with a few to several distal cells evenlydivided by crossveins. Males: Pronotal valve well-developed. Acrotergite bilobed. Pleuritocavae long and curving. Females: Larger individuals sometimes with a few to several distal cells of costal area evenly divided by crossveins.

Autapomorphies.—costal area cells secondarily split by co-linear crossveins near pterostigma.

Distribution.—Brazil, Bolivia, French Guiana, Guyana, Peru, Suriname.

Description.—

Size (mm). Male: length of body 30–41, abdomen 23–30, forewing 39–47, hind wing 34–42, antennae 27–32. Female: length of body 35–37, abdomen 25–29, forewing 46–55, hind wing 40–47, antennae 27–33.

Head. Occiput base color dark reddish brown, pattern often obscured but consisting of irregular diffuse yellow blotches positioned laterally along margin of postorbital sclerite. Vertex sandy to dark earthy brown; setae somewhat dense on anterior surface, becoming more sparse dorsally and posteriorly, moderately long, slender, predominately golden with some brown setae mixed in. Extra-torular sclerites concolorous with frons.

Paraocular band dark brown near antennae and often bordering frons, becoming yellow along orbital sclerite. Frons dark dusky orange, often a diffuse reddish brown sagittal line present, this sometimes incomplete; setae moderately dense, golden to dark brown. Clypeus yellow, laterally with somewhat dark but diffuse and irregular reddish brown maculations. Labrum yellow, concolorous with mesal portion of clypeus, apex sometimes very thinly tinged with brown. Mandibles dull yellow basally, transitioning to very dark reddish brown apically. Labium pale yellow, with a thin dark brown sagittal line, this often very weakly expressed, incomplete, or absent. Eyes large, very slightly dorsoventrally oblong, slightly larger in ventral half, with a very faint mesal flattening posteriorly. Antennae flagellomeres very weakly swollen at nodes, flagellum reddish brown, at least basally, sometimes becoming pale yellowish or darker reddish brown, nodes pale brown to yellowish, verticils only rarely present; clubs very narrow elongate pyriform, apices acuminate, color variable, sometimes posteriorly dark brown with anterior face yellow, sometimes predominately yellowish with anterior face divided by a narrow diffuse longitudinal brown line, sometimes predominately dark brown with yellow portion reduced, covered in fine dark setae.

Thorax. Cervix. Dorsal cervical plate setae golden brown. Cervical sclerite dull dark yellowish brown to dark brown, slightly paler ventrally, becoming yellow toward base. *Pronotum.* Anterior flange a narrow collar, mesally slightly broader, not produced dorsad. Posterior flange of females not quite covering mesoacrotergite, in males valve-like, overlapping acrotergite nearly to posterior margin of mesoprescutum, distal margin with parallel wrinkles oriented toward center point, allowing it to drape slightly over mesoprescutum, ventral surface often with a dense coating of white crystalline material. Pronotum coloration variable, base color dark brown, anterior flange sometimes laterally pale brown or yellow, medial transverse band sometimes mesally with small reddish or yellow maculae, posterior flange in females, dark brown, in males mesally reddish brown, darker in wrinkled portion, often velvety, in both sexes laterally diffusely pale brown or yellow. All surfaces with medium to somewhat long, fine, brown to golden brown setae. *Pteronotum*. In males, distal margin of mesacrotergite produced posterad, flange-like, distinctly bilobed. Dorsal surface of pteronotum proper mostly evenly medium to dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum yellow and occasionally mesal and lateral areas of posterior swelling of mesoscutellum paler or yellow; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, brown to golden brown setae. *Pleuron* base color brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, dark brown on mesanepisternum, otherwise pale yellow, stripes sometimes with a light dusting of pruinescence.

Legs. Femora and tibiae with color variable, mostly pale to dusky yellow, anterolateral surfaces often dusky to considerably dark brown; tarsi very dark brown to nearly black, terminal tarsomere reddish in distal two-fifths. Coxae setae very pale yellow; antennal comb setae golden.

Wings. Dimension and shape. Long, moderately narrow, apex posteriorly weakly subacute. *Venation/cells*. FW. Costal area with subcostal veinlets essentially not inclined, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with four to six forked and unforked pale yellow to brown veinlets; membrane usually pale yellow, sometimes faintly tinted with brown, usually translucent but sometimes weakly opaque, distal margin of pigment straight. Deltus brown, sometimes darkening anteromesally, usually translucent. Presectoral area with ca. nine to twelve cells. Rs with five to six forks. Mp_2 + Cua_1 sharply curving toward hind margin in distal portion. Cubital area with ca. eleven to thirteen irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin somewhat concave, anal angle weakly developed into a process, not yet tooth-like, a single cell row distad of Cup + 1a, cells often undivided by crossveins, but occasionally with as many as three or four distal cells divided. *Color and patterning.* Venation pale to dark brown. Costal and subcostal areas fuscous, pigment sometimes weakly expressed to absent, some individuals with pigment very narrowly absent along anterior margin of costal cells near wing base, some females with costal cells in proximal third of wing darkly margined; subcostal area frequently with at least weak pseudoveinlets, especially in females, these often reduced to anterior spots, particularly in males. Presectoral area in darker individuals with anterior portions of cells subtending R narrowly tinted brown. Apex of wing occasionally very weakly fuscous, with darkest region reduced to anterior portion of apical area. HW. As in forewing except as follows. Costal and subcostal areas usually devoid of pigment, especially in males, but sometimes weakly fuscous, darker in distal half. Mp_2 fork angle approximately 90°. Medial triangle distal domain rather short with one to two cells, sometimes reduced to a single cell. Pre-Cup axillary disk yellow. Pre-Mp_1 area margin very slightly expanded. Anal area with three complete rows of cells. In females, apical one-fifth to one-fourth of wing occasionally weakly to rather distinctly fuscous.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly brown, sometimes distal margin of each tergite with a transverse, narrow diffuse dark brown band; T1 and T2 with moderately dense, moderately long, wispy, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. More or less medium to dark brown, sometimes with diffuse paler to yellowish portions on S1 and S2, these occasionally bearing a thin, dark brown sagittal line, S6 to S8 sometime slightly paler; mostly devoid of long setae, some moderately long, wispy, pale golden setae on S1 and S2. *Pleural membrane*. Reddish to dark brown, often with irregular diffuse yellow mottling or ca. four to five moderately well developed oblique yellow bands, devoid of long setae.

Male terminalia. Unmacerated specimens. Pleuritocavae visible at posterior margin of pleural membrane of segment 7, somewhat elongate and corkscrewing, wrinkled, with dorsal surface very dark and ventral surface often pale or yellow, a second pair often visible at posterior margin of segment 8 but very short, GPC not everted, pulvini not visible, ectoprocts and S9 brown, distal margins sometimes thinly paler yellow. *Macerated specimens.* Pleuritocavae lengths somewhat variable, many times longer than width at base, surface convoluted with a dense coat of microsetae, length of pleuritocava of segment 8 one-third to one-half that of segment 7. S9 apical margin obtusely angled, but angle very shallow, nearly straight. Pulvini very small, unsclerotized, weakly differentiated from gonosaccal membrane, with several, moderately long, very slender, pale setae. GPC somewhat sclerotized; in lateral view dorsal margin weakly arched in basal half, mesally broadly notched, ventrally slightly irregular, dorsal and ventral margins convergent apicad; in ventral view rather broad with an undulating lateral margin. Parameres in ventral view slightly short and broad, proximolateral margins weakly differentiated. Pelta weakly sclerotized, narrowly almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae pale reddish or yellowish to dark brown, distivalvae pale reddish to yellowish brown, ectoprocts dark brown with apical margin sometimes narrowly yellow. *Macerated specimens.* Ventrovalvae in lateral and ventral views elongate and somewhat narrow, length ca. two and a half times width. Linguella only weakly differentiated from surrounding membrane, unsclerotized, bearing several short, stiff, slender, setae. Interdental space more or less round. Interdens sclerotized, with a round base, short, cone-shaped.

Variation. Specimen JRJ_00426 with a few verticils. A few males and females with wings completely faintly tinged with brown pigment, submelanistic. See variation for *costatus.*

Type material examined.—*Holotype* of *luteus* (A1 Fig. 66), male, Brazil, in BMNH collection: “Type /// *luteus* /// luteus Wlk /// JRJ_01634”. Condition: fair; wings spread, antennae and abdomen apex missing, stout pin through mesoacrotergite, head and thorax with numerous holes (dermestids?). *Holotype* of *circumflexus* (A1 Fig. 67), female, Brazil, in BMNH collection: “Type /// Brazil Santarem (back of label: 52 96) ///

circumflexus Wlk /// circumflexus /// JRJ_01635”. Condition: good; wings and antennae spread, no parts missing, antennae glued on, FW margins with some dings.

Additional material examined.—*Bolivia*: Beni Dept (UMMZ: 1 ♀, JRJ_00458). *Brazil*: Amazonas (CMNH: 2 ♀♀, JRJ_00440, JRJ_00443; INPA: 10 ♂♂, JRJ_00430, JRJ_00432, JRJ_00433, JRJ_00437 [A3 Fig. 64], JRJ_00442, JRJ_00455, JRJ_00499, JRJ_00522, JRJ_00523, JRJ_00526, 7 ♀♀, JRJ_00438, JRJ_00441, JRJ_00444, JRJ_00445, JRJ_00448, JRJ_00449, JRJ_00454; UMMZ: 1 ♂, JRJ_00436); Mato Grosso (INPA: 1 ♂, JRJ_00435); Para (CMNH: 1 ♂, JRJ_00518; INPA: 1 ♂, JRJ_00434, 3 ♀♀, JRJ_00439, JRJ_00447, JRJ_00452; MFNB: 1 ♂, JRJ_00498); Roraima (INPA: 1 ♂, JRJ_00431, 1 ♀, JRJ_00446); Santa Catarina (INPA: 1 ♀, JRJ_00450). *French Guiana*: Cayenne (EMEC: 1 ♂, JRJ_00427; UCDC: 1 ♀, JRJ_00428 [A3 Fig. 65]); St Laurent Du Maroni (CMNH: 1 ♀, JRJ_00424); locality uncertain (MFNB: 1 ♂, JRJ_00426, 1 ♀, JRJ_00425). *Guyana*: Cuyuni-Mazaruni (CMNH: 1 ♂, JRJ_00429). *Suriname*: Paramaribo (MFNB: 1 ♂, JRJ_01755); locality uncertain (MFNB: 1 ♀, JRJ_01758; SDEI: 1 ♂, JRJ_01751). *Peru*: Loreto (USNM: 1 ♀, JRJ_00457).

Morphology, biology and ecology.—Some specimens in loan material were collected at lights and light sheets, and at least one was captured in a malaise trap. Few elevations were recorded, these near 100 m.

Discussion.—Some specimens of *luteus* are very similar to *costatus* (see 'Discussion' for *costatus*), but *luteus* is generally larger, has a darker frons, lacks basal verticils, and in males has a slightly wider and longer pronotal valve, a bilobed acrotergite, and well-developed pleuritocavae. *Haploglenius luteus* is nearly identical to the new species *H. brunneus*, but has a yellow labrum and occurs only in the central and eastern parts of northern South America, whereas *brunneus* has a dark brown labrum and occurs in the western parts of northern South America and continues northward through Central America into Mexico.

Van der Weele (1909) determined Gerstaecker's (1885) *pictus* is conspecific with luteus. In Gerstaecker's description he states *pictus* has a yellow labrum. Van der Weele (1909) also made Walker's (1853) *contrarius* a synnym of *luteus*. The type of *contrarius* was viewed briefly at the BMNH but not borrowed for this study, and a JRJ database label was not applied. Penny (1982b) argued that van der Weele (1909) confused *luteus* for *costatus* and made *contrarius* instead a synonym of *costatus*, but van der Weele's descriptions and illustrations agree well with the types and original descriptions of *luteus* and *costatus*, and no confusion appears to have been made.

Navás' (1920) *eurypterus* type was not seen. The original description is of a female. It most closely matches *luteus*—enough characters are described to eliminate most other possibilities. There is a possibility, however, that it represents *brunneus*; Navás doesn't give the color of the labrum. Ábrahám (2013) made it a synonym of *luteus*, and that placement is accepted here. Until the type is seen, it will be treated as a junior subjective synonym of *luteus*.

The type of *circumflexus* was seen and is conspecific with *luteus*.

Haploglenius brunneus *new species*

(A3 Figs. 68–69, 94)

Etymology and nomenclatural notes.—*brunneus*: brunneus (Medieval Latin, perhaps from Proto-Germanic), ‘brown’. In reference to the brown color of the labrum.

Diagnosis.—Frons distinctly darker than clypeus, reddish or smoky amber brown. Labrum dark brown, sometimes only along distal margin. Antennae reddish basally, without verticils. Subcostal area with undulations usually darkened to form pseudoveinlets, especially in FW. FW anal area cell row often with several cells evenlydivided by crossveins. Males: Pronotal valve well-developed. Acrotergite bilobed. Pleuritocavae long and curving. Females: Larger individuals rarely with a few distal cells of costal area evenly divided by crossveins.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—Bolivia, Brazil, Colombia, Ecuador, Mexico, Panama, Peru.

Description.—

Size (mm). Male: length of body 33–38, abdomen 23–27, forewing 38–47, hind wing 34–41, antennae 25–30. Female: length of body 33–38, abdomen 24–25, forewing 47–54, hind wing 41–48, antennae 27–32.

As in *luteus*, except as follows:

Head. Vertex setae predominately dark brown with some golden setae mixed in. Extra-torular sclerites orangish to dark brown. Frons setae dark brown. Labrum evenly medium to dark brown, dorsal margin sometimes narrowly yellow. Mandibles transitioning somewhat sharply to dark brown laterad of dorsal margin of labrum. Antennae flagellum reddish brown, verticils absent; clubs with color variable, often reddish to dark brown, with anterior surface often bearing a narrow, diffuse, longitudinal yellow stripe, but sometimes predominately yellow and anterior surface with a narrow, diffuse, longitudinal dark stripe.

Thorax. Cervix. Cervical sclerite dark brown, narrowly yellow at base. Anterior flange very weakly produced dorsad sublaterally, slightly bilobed. Posterior flange of females covering mesoacrotergite.

Legs. Femora and tibiae base color yellow, pro- and mesothoracic femora mesally to completely dark dusky brown, anterolateral faces of tibiae also dusky dark brown, distal third of femur and proximal third of tibia on anterolateral surfaces of metathoracic leg often slightly darker. Antennal comb setae copper colored with some small black setae along dorsal margin.

Wings. FW. Pterostigma with five to seven veinlets. Deltus often opaque. Presectoral area with ca. nine to thirteen cells. Rs with six to seven forks. Cubital area with ca. eleven to fourteen irregular but more or less complete rows of cells. Anal area cell row often with one to six cells divided by crossveins, mostly but not only in distal portion. *Color and patterning.* Subcostal area usually with pseudoveinlets. Presectoral area in darker individuals with anterior portions of basal three to four cells subtending R narrowly tinted brown. Apex of wing often weakly fuscous, darkest in anterior portion of apical area. HW. Costal and subcostal areas weakly fuscous and darker in distal half to devoid of pigment in males, usually at least weakly fuscous in females. Medial triangle distal domain rather short with one to two cells. Pre-Mp_1 area margin very slightly and broadly expanded. In females, apex of wing often weakly to rather distinctly fuscous.

Abdomen. Sternum. S6 to S8 not paler. *Pleural membrane* with oblique yellow bands, but irregular diffuse yellow mottling not seen.

Male terminalia. Unmacerated specimens. Pleuritocavae elongate and corkscrewing, ventral surface pale or yellow, ectoprocts and S9 brown. *Macerated specimens.* S9 apical margin obtuse but nearly 90°. Pelta apices weakly blunt or truncated.

Female terminalia. Unmacerated specimens. Ventrovalvae, distivalvae, and ectoprocts pale reddish to dark brown.

Variation. Some females very large. Many females and some males with wings completely faintly tinged with brown pigment, submelanistic. Although the head of specimen JRJ_01778 is smashed, the clypeus can be seen clearly and is dull pale yellowish brown with dorsomesal region dusky dark brown.

Variation.—A single anomalous female from Honduras (JRJ_00595) has a yellow frons and yellow labrum.

Type material examined.—*Holotype* (A1 Fig. 68), **new designation**, male, Ecuador, in TAMU collection: "ECUADOR: Napo Prov. Estación Cientifica Yasuní 00°40'28"S, 76°38'50"W IX-5-10-1999, UV light Coll. E. G. Riley, 215 m. /// TAMU - ENTO X0387032 /// HOLOTYPE Haploglenius brunneus Jones ♂ design. J. R. Jones 2014 /// JRJ_00469". Condition: excellent; antennae and wings spread, no parts missing, right FW slightly torn.

Additional material examined.—*Bolivia*: Beni Dept (CMNH: 1 ♂, JRJ_00489; MFNB: 1 ♀, JRJ_01777); Cochabamba (FSCA: 4 ♂♂, JRJ_00482, JRJ_00484, JRJ_00485, JRJ_00488; USNM: 2 ♀♀, JRJ_00491, JRJ_00492); La Paz Dept (FSCA: 1 ♂, JRJ_00483; USNM: 1 ♂, JRJ_00487); Santa Cruz (CMNH: 1 ♂, JRJ_00490; MFNB: 5 ♀♀, JRJ_01770, JRJ_01771, JRJ_01776, JRJ_01780, JRJ_01781; USNM: 1 ♂, JRJ_00486); locality uncertain (MFNB: 1 ♂, JRJ_01775). *Brazil*: Amazonas (CMNH: 3 ♀♀, JRJ_00493, JRJ_00494, JRJ_00495; MFNB: 1 ♀, JRJ_01769; SDEI: 1 ♀, JRJ_01750). *Colombia*: Bogota (MFNB: 1 ♂, JRJ_01778); Valle del Cauca (SDMC: 1 ♀, JRJ_00466). *Ecuador*: Napo (EMUS: 1 ♂, JRJ_00472; UMRM: 1 ♀, JRJ_00467); Orellana (TAMU: 2 ♂♂, JRJ_00470, JRJ_00473); Sucumbios (UCDC: 1 ♀, JRJ_00468 [A3 Fig. 69]; UMSP: 1 ♂, JRJ_00471). *Mexico*: Veracruz (EMUS: 1 ♂, JRJ_00576; FSCA: 1 ♀, JRJ_00459; SDMC: 1 ♂, JRJ_00577). *Panama*: Colon (UCDC: 1 ♀, JRJ_00462); Panama (FSCA: 1 ♀, JRJ_00463; UCDC: 1 ♀, JRJ_00461; USNM: 1 ♀, JRJ_00464; TAMU: 1 ♂, JRJ_00460). *Peru*: Cuzco (MFNB: 1 ♀, JRJ_00479); Huanuco (FSCA: 1 ♀, JRJ_00478); Loreto (MFNB: 2 ♀♀, JRJ_01772, JRJ_01773; UMMZ: 1 ♂, JRJ_00474; USNM: 1 ♂, JRJ_00475); Madre de Dios (DEBU: 1 ♀, JRJ_00481; FSCA: 1 ♀, JRJ_00477; USNM: 2 ♂♂, JRJ_00476); Ucayali (FMNH: 1 ♀, JRJ_00480). *"South America"*: locality uncertain (MFNB: 1 female, JRJ_01784).

Morphology, biology and ecology.—Label data report that one specimen was taken sweeping vegetation, and a few were "on vegetation". Several others were collected at UV lights.

Discussion.—This species is nearly identical to *luteus*; however, it can usually be easily distinguished by the color of the labrum and by distribution. The ranges of the two species do overlap slightly in eastern Peru (and possible in western Brazil and northern Bolivia), and a few specimens in this sympatric region have the labrum brown only along the distal margin, but otherwise yellow.

Confidence in the separation of *brunneus* from *luteus* derives from the considerable degrees of genetic distance observed between other closely related species pairs observed in this study which exhibited similar subtle but consistent levels of phenotypical differences (i.e., *flavicornis-angulatus*, *appendiculatus-juvenilis*), and this also corresponding in one case with a similar geographic division (*appendiculatus-juvenilis*).

A specimen from the Canal Zone, Panama, identified by Eisner and Adams (1975) as *luteus*, was almost certainly *brunneus*.

Haploglenius neoguineensis *Navás, 1914*

(A3 Figs. 70–74, 95)

Haploglenius neoguineensis Navás, 1914

—Navás 1914 r#602: 424, fig. 1 {OD: ♂, DIS. TS: not indicated [holotype by monotypy]. TL: "Novea Guinea: Sarineh" [see "Discussion" below]. TR: "Mus. Matritens" [MNCN]. Type specimen examined (see "Type material examined" below).}

—Sziraki 1998 r#9362: 68 {DIS, GD, L}

—Ábrahám 2013.04.30 r#?????: 176 {JSYN (of *Haploglenius luteus* aberr. *latoreticulatus* van der Weele)}

Haploglenius neognineensis [sic] Navás, 1914

—Navás 1914 r#602: 424 {ISS}

—Sziraki 1998 r#9362: 68 {SYN}

—Ábrahám 2013.04.30 r#?????: 176 {SYN}

Etymology and nomenclatural notes.—neoguineensis: neo- (Latin) 'new' + guinea (from the Berber term "aginaw" via Portuguese) 'Guinea' + -ensis (Latin) 'place of origin': from New Guinea. Named for the mistaken collection locality of the type specimen.

Diagnosis.—Frons distinctly darker than clypeus, reddish or smoky amber brown. Labrum dark brown, sometimes only along distal margin. Antennae with nodes only very weakly swollen. Mesal cells of costal area, at least in HW, wider than their height. Pterostigma distal margins straight. Subcostal veinlets usually diffusely but darkly margined. Subcostal area with undulations usually darkened to form pseudoveinlets. FW anal area cell row undivided by crossveins. Males: Pronotal valve well-developed. Acrotergite bilobed. Pleuritocavae long and curving.

Autapomorphies.—labrum dark brown; FW subcostal area undulations pigmented, forming distinct pseudoveinlets.

Distribution.— Colombia, Costa Rica, Ecuador, Nicaragua.

Description.—

Size (mm). Male: length of body 33–39, abdomen 22–29, forewing 38–43, hind wing 33–38, antennae 25–29. Female: length of body 30–35, abdomen 22–24, forewing 46–50, hind wing 40–43, antennae 25–29.

Head. Occiput base color dark reddish brown, pattern often obscured but consisting of irregular diffuse yellow blotches positioned laterally along margin of postorbital sclerite. Vertex dark sandy reddish brown; setae often slightly denser on anterior surface, only moderately dense overall, moderately long, slender, dark brown with some golden setae mixed in. Extra-torular sclerites pale orange to dark reddish brown, often concolorous with frons. Paraocular band dark brown near antennae and bordering frons, yellow along orbital sclerite. Frons medium to dark dusky orangish or brown, sometimes a very diffuse dark brown sagittal line present, this often incomplete; setae moderately dense, dark brown. Clypeus yellow, laterally with somewhat dark but diffuse and irregular reddish brown maculations. Labrum yellow, darkening to brown in ventral half to two-thirds. Mandibles dull yellow basally, transitioning somewhat sharply to dark brown laterad of dorsal margin of labrum. Labium pale yellow, a thin dark brown sagittal line often present, but sometimes very weakly expressed, incomplete, or absent. Eyes large, entire, very slightly dorsoventrally oblong, very slightly larger in ventral half. Antennae flagellomeres very weakly swollen at nodes, flagellum pale yellowish to reddish brown, nodes paler, verticils absent; clubs very narrow elongate pyriform, apices acuminate, brown, anterior surface often narrowly and diffusely yellow, covered in fine dark setae.

Thorax. *Cervix*. Dorsal cervical plate setae golden brown. Cervical sclerite dark brown. *Pronotum*. Anterior flange a narrow collar, mesally very slightly broader, very weakly produced dorsad, weakly bilobed. Posterior flange of females completely covering mesacrotergite, in males valve-like, overlapping acrotergite nearly to posterior margin of mesoprescutum, distal margin with parallel wrinkles oriented toward center point, allowing it to drape slightly over mesoprescutum, ventral surface often with a dense coating of white crystalline material. Pronotum coloration variable, base color dark brown, anterior flange sometimes anterolaterally paler, medial transverse band sometimes laterally yellowish, posterior flange in females brown laterally, posterolateral margin narrowly yellow, in males mesally dark reddish brown, sometimes darker in wrinkled portion, velvety, posterolateral margin yellow as in females (anterad of articulation in males). All surfaces with medium to somewhat long, very fine, brown setae. *Pteronotum*. In males, distal margin of mesacrotergite produced posterad, flange-like, distinctly bilobed. Dorsal surface of pteronotum proper mostly evenly medium to dark earthy brown and devoid of maculations, except lateral surface of mesoprescutum yellow and occasionally mesal and lateral areas of posterior swelling of mesoscutellum with diffuse yellow maculations; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, golden yellow, stripes occasionally with a light dusting of pruinescence.

Legs. Femora and tibiae base color yellow, pro- and mesothoracic femora mesally to nearly completely dark reddish brown, anterolateral face of prothoracic and sometimes mesothoracic tibiae also dusky reddish brown; tarsi medium to dark reddish brown, almost black, when paler, proximal margins dark brown and tarsi appearing annulated, terminal tarsomere reddish in distal one-fourth. Coxae setae yellow; antennal comb setae copper colored.

Wings. Dimension and shape. Long, moderately narrow, apex posteriorly acute, posterior margins very slightly falcate. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, cells wide, cell height two-thirds to one-half of cell width in proximal half, width becoming narrower than height near pterostigma. Pterostigma with five to six forked and unforked yellow to pale brown veinlets; membrane pale yellow, translucent, distal margin of pigment straight. Deltus brown, anteromesally darkening and becoming slightly opaque. Presectoral area with ca. nine to thirteen cells. Rs with six to seven forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. ten to twelve irregular but more or less complete rows of cells. Cubital triangle distal domain with two to three cells. Anal area hind margin weakly concave, anal angle weakly developed into a process, not yet tooth-like, a single cell row distad of Cup + 1a, cells undivided by crossveins. *Color and patterning.* Venation pale to dark brown. Costal and subcostal areas often at least weakly fuscous, subcostal veinlets usually diffusely margined, at least in proximal two-thirds; subcostal area often with at least weakly expressed pseudoveinlets, these sometimes reduced to anterior spots. Presectoral area with anterolateral portions of basal cells subtending R tinted brown. Apex of wing often weakly fuscous, darkest in anterior portion of apical area. HW. As in forewing except as follows. Mp_2 fork angle approximately 90°. Medial triangle distal domain reduced to a single short cell. Pre-Cup axillary disk yellow. Pre-Mp_1 area margin unexpanded or expansion very slight and broad. Anal area with three complete rows of cells. In some females, apical one-fifth to one-fourth of wing weakly to rather distinctly fuscous.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly brown, often posterior margin of each tergite narrowly and diffusely darkened; T1 and T2 with moderately dense, moderately long, wispy, golden brown setae, remainder of tergum devoid of long setae. *Sternum*. More or less medium to dark brown, sometimes with diffuse paler to yellowish portions on S1 to S3, S1 and S2 occasionally bearing a thin, dark brown sagittal line; mostly devoid of long setae, some moderately long, wispy, golden brown setae on S1 and S2. *Pleural membrane*. Dark brown, occasionally with ca. three to four oblique yellow bands, devoid of long setae.

Male terminalia. *Unmacerated specimens*. Somewhat small pleuritocavae visible at posterior margin of pleural membrane of segment 7, elongate and corkscrewing, wrinkled, with dorsal surface very dark and ventral surface pale or yellow, a second pair often visible at posterior margin of segment 8 but very short, GPC not everted, pulvini not visible, ectoprocts and S9 reddish brown. *Macerated specimens*. Pleuritocavae lengths somewhat variable, many times longer than width at base, surface convoluted with a dense coat of microsetae, length of pleuritocava of segment 8 one-third to one-half that of segment 7. S9 apical margin obtusely angled, but very weakly, nearly straight. Pulvini extremely reduced, nearly indistinguishable from gonosaccal membrane, evidenced by a few short, slender, very pale setae. GPC somewhat sclerotized; in lateral view dorsal margin weakly arched in basal half, mesally weakly notched, ventrally slightly irregular, dorsal and ventral margins convergent apicad; in ventral view rather broad basally, strongly converging apicad, with an undulating lateral margin. Parameres in ventral view somewhat short, proximal margins somewhat well differentiated. Pelta somewhat sclerotized, narrowly almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae reddish to dark brown, distivalvae yellowish brown, ectoprocts brown. *Macerated specimens.* Not available.

Variation. Coloration of tarsi highly variable, with specimens even from the same collection series exhibiting differences; for example, specimen JRJ_00643 has the tarsi nearly black, while specimen JRJ_00642 has the tarsi only medium reddish brown; both were collected from a single locality in Colombia (although over a six week interval). At least one male specimen (JRJ_00643) with wings strongly tinged with brown, submelanistic. At least two females, one from Nicaragua (JRJ_00634—Fig. 73) and one from Costa Rica (JRJ_00637) with the HW apices very darkly fuscous.

Type material examined.—*Holotype* (A1 Fig. 74), male, 'New Guinea' (true locality unknown), in MNCN collection: "Sarmeh, Nva. Guinea /// Typus /// MNCN Cat. Tipos Nº 10606 /// Haploglenius neoguineensis ♂ Nav. Navás S.J. det. /// JRJ_02000". Condition: good, left HW torn.

Additional material examined.—*Colombia*: Valle del Cauca (MFNB: 2 ♂♂, JRJ_00642, JRJ_00643 [A3 Fig. 72]; UNAB: 1 ♀, JRJ_00639). *Costa Rica*: Cartago (BMNH: 1 ♂, JRJ_01637); Guanacaste (JRJC: 1 ♂, JRJ_10182); Heredia (EMEC: 1 ♀, JRJ_00637;

FSCA: 1 ♂, JRJ_00635). *Ecuador*: Los Ríos (FSCA: 5 ♂♂, JRJ_00645 [A3 Fig. 70], JRJ_00646, JRJ_00647, JRJ_00648, JRJ_00649; MFNB: 1 ♂, JRJ_00644); Santo Domingo de los Tsachilas (DEBU: 1 ♂, JRJ_00636; UCDC: 1 ♀, JRJ_00650; UMRM: 1 ♀, JRJ_00641 [A3 Fig. 71]; USNM: 1 ♀, JRJ_00638); locality uncertain (BMNH: 1 ♂, JRJ_01638). *Nicaragua*: Rio San Juan (TAMU: 1 ♀, JRJ_00634 [A3 Fig. 73]).

Morphology, biology and ecology.—Onore et al. (2014) reported collecting specimens (identified as *H. latoreticulatus*) at lights at the Otongachi field station in Ecuador. They also observed live males signaling with the pronotal valve (see discussion of the valve under 'Morphology', above) amongst shaded tree roots during the day.

Several specimens in loan material were collected at UV lights. Collection site elevations ranged from 50 to 1650 m.

Discussion.—The geographic origin of *neoguineensis* has been reflected on by numerous authors (New 1986; Tjeder 1992: 60; Sziraki 1998; Ábrahám 2013), with the notion having been expressed in one form or another that Navás's type was mislabeled. Navás himself, in his original description (1913: 425), recognized in OD that all other species in the genus were American. The type specimen was examined for this study and is conspecific with specimens originating from northwest South America (northwest of the Andes) and continuing into Central America.

This species is similar in some regards to *reticulatus* (see ‘Discussion’ for *reticulatus*), but is not conspecific with it; it differs in the males having a well-developed pronotal valve and bilobed mesoacrotergite, features that instead signal the affinity of this species to *luteus* and *brunneus*.

Haploglenius handlirschi ***van der Weele, 1909***

(A3 Figs. 75–77, 95)

Haploglenius handlirschi van der Weele, 1909

—van der Weele 1909.01.05 r#420: 46, fig. 18 {OD: ♂♀, D, DIS, ET, MOR, SR. TS: indicated as a syntype series (but lectotype designated by Ábrahám 2013). TL: ‘northeast Brazil’ (but see “Discussion” below). TR: not indicated [NMW and MZPW]. Type specimen examined (see “Type material examined” below).}

—Navás 1912b.10.31 r#542: 208 {D, GD, K, SR}

—Navás 1913 r#1207: 47 {D, GD, K, SR}

—Banks 1924.01.?? r#76: 437 {MOR}

—Navás 1929.02.?? r#860: 107, 109 {D, GD, L}

—Shetlar 1977 r#5727: 93 {Ph.D. dissertation, nomenclatural acts invalid: DIS}

—Penny 1978.09.15 r#5098: 13 {GD, L}

—Penny 1982b r#5103: 624 {D, MOR}

—Ábrahám 2013.04.30 r#?????: 179, fig. 6 {GD, TL, TR, TS}

Etymology and nomenclatural notes.—*Handlirschi;* a Latinized noun. Named by van der Weele for Mr. Anton Handlirsch, curator of the Imperial Natural History Court Museum in Vienna.

Diagnosis.—Large species, especially females (FW 46–56 mm). Width of costal cells equal to or narrower than height. Pterostigma veins dark brown; membrane pigment evenly dark brown, often extending past pterostigma along margin into apical area. FW anal angle very slightly developed, hind margin distad only very slightly concave. FW anal area cell row divided by oblique crossveins. Males: Pronotal valve poorly developed, not articulable. Pleuritocavae hardly developed, not visible in unmacerated specimens.

Autapomorphies.—labrum dark brown; male pronotum flange dorsally evenly medium brown; basal cell of HW costal area opaque over entire surface, dark reddish brown; pterostigma pigment dark, distinctly spilling out into apical area distally; very small pouch-like pleuritocavae present on segment 8.

Distribution.—Eastern Brazil, Honduras (?), Mexico (?) [see 'Discussion' below].

Description.—

Size (mm). Male: length of body 37–39, abdomen 27–30, forewing 46–47, hind wing 41–44, antennae 28–29. Female: length of body 37, abdomen 26, forewing 54–56, hind wing 48–51, antennae 30.

Head. Large. Occiput base color medium to dark reddish brown, an elongate diffuse yellow macula positioned laterally along margin of postorbital sclerite. Vertex sandy orange to dark brown; setae often slightly denser on anterior surface, only moderately dense overall, moderately long, slender, slightly wavy, dark golden brown with some pale yellow setae mixed in anteriorly. Extra-torular sclerites medium to dark reddish brown. Paraocular band nearly entirely dark brown, narrowly yellow along frons near margin of clypeus, orbital sclerite sometimes thinly pale. Frons dusky medium orangish to dark brown, a diffuse dark brown sagittal line present; setae moderately dense, moderately long, slender, very pale yellow or white with some dark brown setae mixed in. Clypeus yellow, laterally often with a somewhat diffuse dark brown maculation. Labrum very dark brown. Mandibles dull yellow basally, transitioning to dark reddish brown in apical half. Labium pale yellow. Eyes large, very slightly dorsoventrally oblong, with a very faint posteromesal flattening. Antennae flagellomeres in distal half with nodes very weakly expanded, flagellum reddish brown, base of each flagellomere and distal margin of each node pale, verticils absent; clubs elongate pyriform, weakly acute, nearly completely yellow, anterior face often narrowly and diffusely brown to dark brown, covered in fine pale setae.

Thorax. Cervix. Dorsal cervical plate setae pale yellow. Cervical sclerite predominately yellow, dorsally dark brown. *Pronotum.* Anterior flange somewhat narrow, slightly produced dorsad. Posterior flange of female barely covering mesoacrotergite, in males nearly identical to female, except sublaterally very weakly articulated (but not valve-like), presence of white crystalline material on ventral surface uncertain, presumably absent. Pronotum base color dark brown, anterior flange anterolaterally narrowly paler, medial transverse band with some small, irregular maculations mesally, posterior flange evenly brown, posterolateral margin narrowly yellow or orange. All surfaces with moderately long, very fine, golden brown setae. *Pteronotum*. Evenly medium to dark earthy brown and mostly devoid of maculations, except lateral surface of mesoprescutum yellow and usually mesal and lateral areas of posterior swelling of mesoscutellum with very faint diffuse yellow maculations; velvety spots of metascutum dark brown, inconspicuous; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color dark brown, a pair of yellow stripes descending obliquely anterad from wing bases to venter; pleural setae somewhat dense, moderately long, slender, white.

Legs. Femora almost completely dusky brown, narrowly and diffusely yellow on distal portions of dorsal and posterolateral faces; tibiae dusky brown anterolaterally, yellow posterolaterally; tarsi dark reddish brown to almost black, terminal tarsomere pale reddish or orange in distal one-fourth. Coxae setae white; antennal comb setae golden.

Wings. Dimension and shape. Long, somewhat slender, apex posteriorly weakly acute. *Venation/cells.* FW. Costal area with subcostal veinlets essentially not inclined, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with six to seven forked and unforked dark brown veinlets, these sometimes margined with dark brown pigment; membrane evenly dark brown, translucent, distal margin of pigment slightly produced one cell width along Sc+R, many cell widths along wing margin in apical area. Deltus brown, anteromesally darkening and becoming slightly opaque. Presectoral area with ca. twelve to fourteen cells. Rs with six forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. nine to twelve irregular but more or less complete rows of cells. Cubital triangle distal domain with three cells. Anal area hind margin very weakly concave, nearly straight, anal angle very weakly developed into a process and not yet tooth-like, a single cell row distad of Cup + 1a, but cells divided by oblique crossveins in distal two-thirds. *Color and patterning.* Venation pale to dark brown. Costal and subcostal areas lightly fuscous, with pigment narrowly absent along anterior margin of costal cells, C very narrowly margined in proximal half of wing with dark brown pigment; subcostal area with undulations faintly darkened, but not expressed as distinct pseudoveinlets. Remainder of wing devoid of pigment, except in apical area near pterostigma, brown fuscous pigment of pterostigma often continuing along wing margin several cell widths. HW. As in forewing except as follows. Mp_2 fork angle slightly less than 90°. Medial triangle distal domain with two cells. Pre-Cup axillary disk yellow, anteroproximal margin diffusely dark brown. Pre-Mp_1 area margin unexpanded. Anal area with three complete rows of cells.

Abdomen. In males usually not quite reaching to pterostigma with wings folded back; in females, not reaching to pterostigma, much shorter. *Tergum*. Evenly brown; T1 and T2 with moderately dense, long, wispy, pale golden yellow setae, remainder of tergum devoid of long setae. *Sternum*. More or less evenly medium to dark brown; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, sometimes with ca. three to four oblique yellow bands, devoid of long setae.

Male terminalia. Unmacerated specimens. Pleuritocavae not evident, GPC not everted, pulvini not visible, ectoprocts and S9 dark brown. *Macerated specimens.* Pleuritocavae only very weakly formed or absent, pleural membrane of posterior margin of segment 7 very slightly pouched, pleural membrane of posterior portion of segment 8 very weakly pouched, pleuritocavae absent. S9 apical margin obtusely angled, but very weakly, nearly straight. Pulvini small, not sclerotized, weakly differentiated from gonosaccal membrane, bearing several moderately long, slender, brown setae. GPC somewhat weakly sclerotized; in lateral view dorsal margin weakly arched in basal half, subapically distinctly notched, notch short but rather deep, ventrally more or less entire, dorsal and ventral margins convergent apicad; in ventral view rather broad basally, converging apicad, with very weakly undulating lateral margins. Parameres in ventral view somewhat short, proximal margins somewhat weakly differentiated. Pelta sclerotized, narrowly almond shaped.

Female terminalia. Unmacerated specimens. Ventrovalvae, distivalvae, and ectoprocts brown. *Macerated specimens.* Ventrovalvae in lateral and ventral views somewhat elongate and narrow, length ca. two times width. Linguella only weakly differentiated from surrounding membrane, unsclerotized, bearing several short, stiff, slender, setae. Interdental space small, more or less round. Interdens sclerotized, short, cone-shaped.

Variation. Specimen JRJ_00581 with clypeus dark brown, slightly paler laterally, labrum and labium dusky orangish brown, cervical sclerite dull dark brown. At least one male (JRJ_01753—Fig. 75), from Brazil, with fuscous areas and pterostigmata somewhat paler, but apparently not teneral.

Type material examined.—*Syntype* (A1 Fig. 77), female, "Honduras" (Brazil? see "Discussion" below), in NMW collection: "Honduras San Pedro Sula ex coll. Fruhstorfer /// ♀ /// Handlirschi vdWeele type det. v.d.Weele /// JRJ_00582". Condition: excellent; antennae and wings spread, antennae missing, a large blob of brown glue among legs, abdomen apex removed for dissection, genitalia in vial with specimen.

Additional material examined.—*Brazil*: Pernambuco (MFNB: Brazil, 1 ♂, JRJ_01753 [A3 Fig. 75], 1 ♀, JRJ_01757 [A3 Fig. 76]); Rio de Janeiro (FSCA: 2 ♂♂, JRJ_00583, JRJ_00584). *Mexico*: locality uncertain (MHNG: 1 ♂, JRJ_00581).

Morphology, biology and ecology.—Label data of loan material provides no information on collecting conditions. Nothing is known about the biology of this large and distinctive species.

Discussion.—Van der Weele, in his original description, discussed his syntype series and did not designate a holotype. Ábrahám (2013) designated a lectotype and paralectotype from material housed at the MZPW. One of the van der Weele's syntypes was discovered in loan material sent from NMW and was examined for this study. It is a female with a locality label indicating it is a Fruhstorfer specimen collected in San Pedro Sula, Honduras. Van der Weele (1909) considered this specimen to be among those in Fruhstorfer's collection that have appear to have had labels switched and are thus mislabeled (see "Discussion" for *A. vacua*, above). He suggested the specimen originated instead from Espiritu, Santo Brazil, and gave in his original description as distribution for the species northeast Brazil. If the Fruhstorfer specimen truly originated from Honduras, it would indicate that *handlirschi* has one of the broadest distributions of a species of *Haploglenius*. As most specimens discovered in this came from Brazil and very little has been said about the distribution of *handlirschi* in the literature, its true distribution is not yet certain. However, a single male examined from the MHNG collection and originating from the collection of Pictet gives "Mexique" as its origin.

Haploglenius legnotos *new species*

(A3 Figs. 78, 93)

Etymology and nomenclatural notes.—*legnotos*: legnotos (Greek), 'with a colored border'. Named for the brown stripe subtending R in the FW.

Diagnosis.—Wings long and slender. Pterostigma veins dark brown, pigment yellow. Cell row subtending R in both wings infuscated with dark brown pigment, this extending past pterostigma to fill most of apical area. Two rows of cells in the HW anal area. Male: Unknown.

Autapomorphies.—None determined in cladistic analysis.

Distribution.—French Guiana.

Description.—

Size (mm). Female: length of body 28, abdomen 20, forewing 40, hind wing 34, antennae 20.

Head. Breadth at widest point (of eyes) slightly superequal to width of mesothorax at wing base. Occiput dark brown, laterally with some small, diffuse, irregular brownish yellow maculations. Vertex dusky brown; setae rather sparse, moderately long, dark brown. Extra-torular sclerites dark brown. Paraocular band black near antennae, otherwise dusky brown. Frons dusky brown; setae moderately sparse, dark brown. Clypeus dull dusky yellowish with a diffuse reddish brown sagittal line, some dark reddish brown maculations present sublaterally and along dorsal margin. Labrum slightly darker than mesal portion of clypeus. Mandibles dull yellow basally, transitioning to very dark reddish brown apically. Labium concolorous with base of mandibles, with a thin dark brown sagittal line. Eyes very slightly dorsoventrally oblong but symmetrical, with only a very faint mesal flattening. Antennae shorter than in congeners, not reaching to second fork of Rs in spread individual, flagellomeres shape undifferentiated, flagellum brown, nodes paler; clubs elongate pyriform, dark brown, anterior face yellow, yellow region divided by a diffuse sagittal brown stripe, covered in fine dark setae; verticils absent.

Thorax. Cervix. Dorsal cervical plate setae golden. Cervical sclerite dark brown. *Pronotum.* Anterior flange narrow, slightly produced dorsad. Posterior flange produced dorsoposteriorly, covering mesoacrotergite. Pronotum coloration evenly brown. All surfaces with somewhat long, fine, golden brown setae. *Pteronotum*. Dark earthy brown; velvety spots of metascutum dark brown; entire surface of pteronotum covered with moderately dense, moderately long, fine, golden brown setae. *Pleuron* base color brown, a pair of oblique pale brown stripes descending from wing bases to venter; pleural setae moderately dense, medium length, very fine, golden brown.

Legs. Pro- and mesothoracic legs dusky reddish brown, posterolateral surfaces paler, yellow, metathoracic legs entirely yellowish; tarsi black, distal two-fifths of terminal tarsomere diffusely reddish, tibial spurs more or less straight, posterior spur slightly longer than anterior one and not extending past third tarsomere on pro- and mesothoracic legs, second tarsomere on metathoracic leg. Coxae setae pale yellow; antennal comb setae copper-colored, a few black ones distributed along anterior distal margin.

Wings. Dimension and shape. Long, slightly narrow, apex posteriorly subacute. *Venation/cells.* FW. Costal area with subcostal veinlets not inclined, cell width and height more or less coequal in proximal half, width narrowing to ca. half of height in distal half. Pterostigma with six forked and unforked pale brown veinlets; membrane pale yellow, translucent, distal margin of pigment straight. Deltus dark brown, becoming opaque anteriorly. Presectoral area with nine (left wing) to eleven (right wing) cells. Rs with six forks. Mp_2 + Cua_1 somewhat sharply curving toward hind margin in distal portion. Cubital area with ca. ten to twelve irregular but more or less complete rows of cells. Cubital triangle distal domain with three cells. Anal area hind margin essentially straight, (left wing very slightly convex, right wing very slightly concave), anal angle not developed into a process, a single cell row distad of Cup + 1a, with cells undivided by crossveins. *Color and patterning.* Venation dark brown. Costal and subcostal areas fuscous, pigment narrowly absent along anterior margin. Presectoral and radial area with anterior portions of cells in row subtending R tinted brown, forming, with costal and subcostal area pigment, a stripe from wing base to apical area. Apical area of wing almost completely darkened with brown pigment. HW. As in forewing except as follows. Mp_2 fork angle acute. Medial triangle distal domain somewhat elongate, with three cells. Pre-Cup axillary disk dark brown. Pre-Mp_1 area margin not expanded. Anal area with two complete rows of cells.

Abdomen. Not reaching to pterostigma, much shorter. *Tergum*. Evenly dark earthy brown; T1 and proximal portions of T2 with moderately sparse, moderately long, wispy, pale golden setae, remainder of tergum devoid of long setae. *Sternum*. Evenly dark earthy brown; mostly devoid of long setae, some moderately long, wispy, pale yellow setae on S1 and S2. *Pleural membrane*. Dark brown, devoid of long setae.

Female terminalia. Unmacerated specimens. Ventrovalvae, distivalvae, and ectoprocts dark brown. *Macerated specimens.* Not available.

Type material examined.—*Holotype* (A1 Fig. 78), **new designation**, female, French Guiana, in FSCA collection: "FRENCH GUIANA: 17 km W of N2 on Belizon Rd, 3-XII-2002, J. E. Eger /// N04°17.825' W052°22.812' 94m MV Light /// HOLOTYPE Haploglenius legnotos Jones ♀ design. J. R. Jones 2014 /// JRJ_00622". Condition: excellent; antennae and wings spread, no parts missing, HWs slightly torn.

Additional material examined.—None available.

Morphology, biology and ecology.—The holotype was collected at a UV light at low elevation (94 m).

Discussion.—Although this species generally resembles other New World haplogleniines, its taxonomic affinities are difficult to determine. Placement in the phylogeny was questionable, as male characters are lacking, and it was ultimately removed. Prior to removal it was placed basad of *procerus*. Like *Neascalobyas* and *Ascalobyas* it has short antennae and only two rows of cells in the anal area of the HW. But its wings are long and slender like *H. extensus*, with which it also shares a longitudinal stripe on the wings and pigmented apical areas. The FW anal areas of these two species are also almost identical in shape and venation. But the apical margin of the pterostigma of *legnotos* is straight, completely unlike the distinctly crescent shape in *extensus* and other members of its species group, and the pteronotum lacks stripes. Collection of males could help determine its place within the NWH.

Removed from **Ascaloptynx**

oligocenica Nel, 1990† new status

incertae sedis within Haplogleniinae **new status**

Ascaloptynx oligocenica Nel, 1990

—Nel 1991. ??.?? r#8267: 328, figs. 1–8 {OD: abdomen missing, sex uncertain, BG, D, DIS, MOR. TS: holotype by original designation. TL: "Stampien supérieur, lamanites de Cereste, Alpes-de-Haute-Provence, France". TA: Oligocene. TR: MNHN, Institut de Paleontologie. Type specimen examined (see "Type material examined" below).}

Etymology and nomenclatural notes.—*oligocenica*: Latinized noun. Named for the age of the rock layer in which the fossil was discovered.

Type material examined.—*Holotype*, abdomen missing, France, in MNHN collection, Institute of Paleontology. Condition: good, compression fossil, entire.

Additional material examined.—Additional specimens beyond the type are unknown.

Discussion.—The holotype fossil was examined and photographed for this study. There were a few notable differences between the specimen and the illustrations provided in the original description. First, the developed FW anal processes shown in Nel's illustrations are not actually present in the fossil impression in either wing. The original specimen may have once possessed them, but no evidence was found in the physical impression, despite repeated attempts to improve visual contrast (wetting the surface with ethanol and placing the light source at strongly oblique angles). Second, the mesal cells of the right HW apical area are misdrawn to suggest they are elongate and curved and that Sc+R and the apical area are naturally bent (and the apical area margin, which is missing, is also drawn in). But in the impression, the posterior half of the wingtip is clearly torn and offset.

The specimen does seem to be a haplogleniine owlfly. The outer eye shells are missing, but the eyes appear to be entire based on the circular shape of the ocular diaphragms. Nel provided a reasoned discussion of the probable identity of the fossil by comparing it to each of the extant genera of Haplogleniinae with narrowed wing bases and a well-developed FW anal process (which genera he included under a misinterpreted Verticillecerini Orfila, 1949). Although the shape of the anal angle cannot be demonstrated, the FW is narrowed, and in all extent species with a narrowed FW, the basiposterior margin is drawn into a process, so a placement with other genera having a well-developed process is a fair assumption to make. The impression of the process (in both wings) may simply have been lost over time.

Compared to extant species in the *appendiculatus* species group (ASG), the wings of *oligocenica* are rather broad. The fossil also expresses other very subtle differences with extant species. The scape setae are much thicker and darker than in any of the three ASG species. The antennae are longer in *oligocenica*, in which they reach past the second fork of Rs, than in ASG species, in which they only reach past the first fork of Rs. The tarsus setae are robust and dark, and match that on the venter of the ASG tarsus, but not the dorsum. It is possible the tarsus of the fossil rolled and became inverted during preservation. The apical area cells are not as finely divided in *oligocenica* as in the ASG; nor are the costals subapically divided, as in *appendiculatus* and *juvenilis* (but not *elongatus*). Perhaps most diagnostically, the nodes and internodes of the antennae of *oligocenica* do not appear to be setose, an important consideration in light of the fact that in ASG the setae are more robust that in all other NWH. However, the antennal impressions of *oligocenica* are rather weak and may not have been preserved well; the clubs, for example, also show no setae. But, again, they are rather well-preserved, and one would expect to see at least some faint impressions, particularly considering that setae on other parts of the body are well-registered.

A final consideration to make in determining the correctness of a placement of *oligocenica* within the ASG is the probable age of the two taxa. The ASG is a highly derived lineage within *Haploglenius*. Despite being on a long branch, its position within the genus is supported by several synapomorphies and by molecular data (chapter 4). Although a phylogeographic analysis was not conducted in this study, based on the results of the cladistic analysis and available morphological data, it is reasonable to infer that the divergence of the *appendiculatus* species group occurred late in the evolution of the NWH from South and/or Central American progenitors (see 'Discussion' for *elongatus*, above). In this case, these progenitors probably entered Central America after the joining of the isthmus to South America sometimes in the Pleiocene, approx. 4 MYA. Nel's hypothesis, on the other hand, places *Ascaloptynx* in Europe during the Oligocene, approx. 23 to 38 MYA.

In spite of the strong general similarities in wing shape and venation (high congruence is also found in the wings of *Paramoeridops* Tjeder 1992, and *Balanopteryx* Karsch, 1889), features that would confidently place *oligocenicus* in the ASG are at least subtly different, or absent (antennae: setae; FW axillary angles; legs: setosity; abdomen: size, shape, setosity and maculation patterns). For these reasons, as well as the distinct discrepancy in hypothesized geologic ages of the taxa, it is here inferred that the fossil *oligocenicus* represents a relict entire-eyed owlfly ancestor much more ancient than the putatively geologically recent ASG. A robust higher-level analysis that includes molecular data and infers divergence times may be needed to corroborate or revise this hypothesis. Until then, oligocenica is removed from *Ascalaptynx* (and thereby *Haploglenius* and the ASG) and is placed *incertae sedis* within Haplogleniinae.

Final thoughts and future research

Taxonomic revisionary work and cladistic analysis presented in this paper has resulted in the following revised classification for the NWH:

Haplogleniinae of the Western Hemisphere

Amoea Lefèbvre, 1842

arenosa (Walker, 1853)

chlorops (Blanchard in Blanchard and Brullé, 1845)

flavitaenia n. sp.

immaculata (Olivier, 1790)

impediens (Walker, 1853)

iniqua (Walker, 1853)

latipennis (Navás, 1912)

nivea Navás, 1911

periculosa n. sp.

vacua (Gerstaecker, 1894)

Neascalobyas n. gen.

machadoi (Penny, 1982)

nigrantia n. sp.

Ascalobyas Penny, 1982

microcerus (Rambur, 1842)

oswaldi n. sp.

Haploglenius Burmeister, 1839

appendiculatus new species group

appendiculatus (Fabricius, 1793)

elongatus n. sp.

juvenilis (McLachlan, 1871)

gerstaeckeri new species group

gerstaeckeri (van der Weele, 1909)

acuminatus n. sp.

extensus new species group

cuboides n. sp.

decoratus n. sp.

decorus Ábrahám, 2013

extensus Banks, 1924

flavicornis new species group

angulatus Gerstaecker, 1894

flavicornis McLachlan 1871

reticulatus new species group

abdominevittatus Ardila and Jones, 2012

aquilonius n. sp.

reticulatus Navás 1923

species not placed into a species group

brunneus n. sp.

costatus (Burmeister, 1839)

handlirschi van der Weele, 1909

legnotos n. sp.

luteus (Walker, 1853)

neoguineensis Navás, 1914

normani n. sp.

peruvianus van der Weele, 1909

procerus n. sp.

The cladistic results in this work were generated exclusively from morphological data and represent hypotheses of monophyly to be tested further. Although some clades were well-supported (monophyly of NWH, *Haploglenius*, ASG, FSG, ESG, inclusion of ASG within NWH), others had minimal support (internally within *Amoea*, monophyly of RSG, position of ASG within NWH) and may require additional reinforcement. Also, some outstanding questions were only weakly addressed, namely the position of the NWH within the Haplogleniinae. In the last case, higher-level analysis including many more genera from within the subfamily will be required to determine the correct position. In all cases, the addition of more morphological characters and molecular data should provide opportunities for such corroboration and/or correction. Assuming topologies continue to show complete resolution and high support, biogeographic analysis should be pursued in order to enlarge our understanding of the geographic distribution patterns and hypothetical ancestral radiations (e.g, ASG and *Amoea* dispersing across the isthmus and colonizing North America from a South American origin).

Despite the above shortcomings, this work provides increased nomenclatural and taxonomic stability to a group that has historically been fraught with numerous uncertainties. Many synonymies have been confirmed or created as a result of examinations of type material. *Amoea* has been demonstrated to be a primitive and widespread genus with distinct species. A new small genus, *Neascalobyas*, has been discovered. The phylogenetic positions of the (previously) taxonomically problematic *appendiculatus* species group and *H. abdominevittatus* have been determined. *Haploglenius* has been revealed to be a widespread and species-rich genus containing several highly derived lineages. And thirteen new species of NWH, many with very narrow distributions, have been described.

CHAPTER V

OWLFLYLOGENY: FIRST PHYLOGENY OF THE OWLFLIES (NEUROPTERA: ASCALAPHIDAE) BASED ON MORPHOLOGICAL AND MOLECULAR EVIDENCE

Synopsis

The first large-scale phylogeny of the Ascalaphidae (owlflies) is presented. A combined morphological (25 characters) and molecular (16S, 18S, and COI genes) dataset was analyzed under several analytical regimes (maximum likelihood, Bayesian, and parsimony) for 76 exemplars of Myrmeleontiformia (Ascalaphidae, Myrmeleontidae, Nemopteridae, Nymphidae, Psychopsidae), including 57 of Ascalaphidae. At the superfamily level, the families were recovered in all analyses in the form Psychopsidae + (Nymphidae + (Nemopteridae + (Myrmeleontidae + Ascalaphidae). Ascalaphidae was recovered as monophyletic in the Bayesian and parsimony analyses, and paraphyletic with respect to Ululodini and Myrmeleontidae in the maximum likelihood analysis. The subfamilies Haplogleniinae and Ascalaphinae were not recovered as monophyletic in any analysis. The Ululodini were monophyletic and well-supported in all analyses, as were the New World Haplogleniinae and the African/Malagasy Haplogleniinae. The remaining Ascalaphidae, collectively, were also consistently monophyletic, and include a genus traditionally placed in Haplogleniinae, *Protidricerus* van der Weele. None of the included tribes of non-ululodine Ascalaphinae were monophyletic in any analysis.

Protidricerus was discovered to express a well-developed pleurostoma, a feature previously only encountered in divided-eye owlflies, and this feature may be important in future classifications. The feature traditionally used to differentiate the Haplogleniinae and Ascalaphinae, the entire or divided eye, can no longer be regarded as a reliable spot-diagnosis character to separate monophyletic groups within the family, and should be reevaluated.

Introduction

Ascalaphidae, or “owlflies”, are found worldwide, and are highly specialized aerial predators of other flying insects. They come in many shapes and sizes, but generally resemble small to medium-sized dragonflies in the shape of the body and wings and in the inclination of the thorax and legs. Many species are only active at dusk or nocturnally. As larvae, they are sit-and-wait predators that capture passing arthropods in their sharp-tipped jaws and immobilize them with paralytic venom before carefully sucking out their internal fluids.

Owlflies are members of the superorder Neuropterida, or “lacewings”. They are usually easily distinguished from other lacewings by their large size, huge eyes, long antennae, and often very setose bodies. Yet, within the family there are many exceptions to this fundamental corporal presentation. Their distinctive morphology has been recognized for some time. Fabricius (1775) was the first to unambiguously separate them from dragonflies and butterflies, placing *Myrmeleon barbarum* Linnaeus in his new Neuroptera (sensu latu) genus *Ascalaphus*, which he differentiated from *Hemerobius* Linneaus, 1758 and *Myrmeleon* Linneaus, 1767. Today there are over 450 valid described species in ca. 100 genera, 15 tribes, and three subfamilies (Oswald 2013).

Some putatively primitive Neuroptera are ascalaphid-like and have presented placement challenges to taxonomists. Newman (1838) placed his short-antennaed Australian genus *Stilbopteryx* in "Myrmeleonites" (=Myrmeleontidae, or "antlions"), stating it was "evidently related to *Ascalaphus* and *Myrmeleon*". Lefebvre (1842) described a second closely related species of *Stilbopteryx* (as *Azesia napoleo*), and placed it instead in the Ascalaphidae (it was later moved to *Stilbopteryx* by Hagen 1866). Apparently, due to the specimen lacking them, Lefebvre drew in rather long antennae on his figure of *A. napoleo*, confusing subsequent authors (McLachlan 1871 later caught the error). Hagen (1866) considered *Stilbopteryx* to belong to the Myrmeleontidae because of the elongate cells of the apical area. McLachlan (1871) followed this placement, but on account of the presence of the Eltringham's organ at the base of the hind wing, a trait seen in many antlions. Van der Weele (1903) described another similar Brazilian species in his new genus *Albardia* and placed it with the "holophthalmous Ascalaphidae". *Albardia* is very much like *Stilbopteryx* in its large size, short antennae, head morphology, short prothorax and legs, large elongate wings with a curved Cua, and broad, densely veined apical areas. Van der Weele (1909) felt these similarities were so strong that he placed *Albardia* and *Stilbopteryx* together in his new subfamily Protascalaphinae. Tillyard (in

Hacker 1913) stated that *Albardia* and *Stilbopteryx* represent ‘an archaic group standing near the base of the phylogenetic stem out of which both the ascalaphids and myrmeleontids arose”. Later, Tillyard (1926) removed them from Ascalaphidae and placed them together in his new family Stilbopterygidae. More rearrangements followed: Kimmins (1940) moved *Stilbopteryx* to the Myrmeleontidae in subfamily Stilbopteryginae, reasoning it is closely related to the Palparinae. Riek (1968, 1976) described a new Australian genus *Aeropteryx* and new species of *Stilbopteryx*, and followed Tillyard in grouping *Albardia* and *Stilbopteryx*, with his new genus *Aeropteryx*, in Stilbopterygidae, pending a larger review of the Ascalaphidae and Myrmeleontidae. Finally New (1982), in his review of the Stilbopterygidae, compared genitalic structures, forewing venation, and abdomen length, and decided the genera within the family constituted two distinct groups. He placed *Stilbopteryx* and *Aeropteryx* into the Myrmeleontidae as subfamily Stilbopteryginae, on the basis of the posteromesal portion of female sternite VIII (the linguella) being “strongly reduced”, and in the posterior gonapophysis lobe being “strongly developed”. He placed the monobasic *Albardia* into the Ascalaphidae as subfamily Albardiinae on the basis of the posteromedial portion of sternite VIII being well-developed, stating, however, that *Albardia* is “not clearly allied with other described members”. This classification continues to the present.

Though clearly taxonomically vexing, these placements have not previously been rigorously evaluated in an explicitly phylogenetic framework. In fact, virtually no phylogenetic research to date has focused on the Ascalaphidae. Several works have touched upon the Ascalaphidae and Myrmeleontidae together, but all within higher level treatments of the entire order. The Ascalaphidae have long been inferred to belong to a small group of similar families within the Neuropterida variously called Myrmeleonoidea (e.g.,Withycombe 1925), Myrmeleontoidea (e.g., New 1991) and Myrmeleontiformia (MacLeod 1964, Aspöck et al. 2001, Winterton 2010). The term Myrmeleontiformia (referring to the families Psychopsidae, Nymphidae, Nemopteridae, Myrmeleontidae, and Ascalaphidae), because of its more recent and common usage among currently practicing neuropterologists (e.g, Winterton 2010, J. Oswald pers. comm.), is preferred here. In every study Ascalaphidae have been placed together with Myrmeleontidae, in what is here termed the Ascalaphidae-Myrmeleontidae complex (AMC). Hypotheses of the exact relationship of these two families to the others within the Myrmeleontiformia have changed with time. Handlirsch (1906-1908) was among the first to present a phylogeny for the Neuropterida, basing his ideas on fossil evidence. He proposed a close relationship between the AMC and Nymphidae (Fig. 1A), with the Nemopteridae tenuously placed in an unresolved basal position. Withycombe (1925) was the first to unambiguously place these four families together in a group he called Myrmeleonoidea, flanked by the Psychopsidae (Fig. 1B), on the basis of toothed larval jaws and the presence of dolichasters—the specialized scale-like dorsal setae of the larvae—as well as other features (eggs, internal anatomy, etc.). He regarded the Nemopteridae as "peculiar" for some of its outlying features (e.g., jaws not toothed). He also considered *Stilbopteryx* and *Albardia* to be transitional "Protascalaphine forms" between the Myrmeleontidae and Ascalaphidae. Aspöck et al. (2001) were the first to apply to the question modern phylogenetic analysis techniques using computer software (Hennig86) that analyzed a morphological dataset of 36 adult and larval characters represented by single family exemplars. They found strong evidence for a monophyletic “Myrmeleontiformia” (Fig. 1C). Haring and Aspöck (2004—Fig. 1D) presented a distance tree based on the cytochrome oxidase III gene that also recovered a monophyletic Myrmeleontiformia; it placed Nemopteridae as sister to the AMC, but did not include Nymphidae. Aspöck and Aspöck (2008) proposed an altogether different phylogeny based on a large dataset of genitalic characters (Fig. 1E); they placed Nemopteridae in a clade with Psychopsidae + Nymphidae. The most recent and comprehensive analysis of the Neuropterida was performed by Winterton et al. (2010—Fig. 1F–I), who analyzed a combination of 55 morphological characters and four genes under several different theoretical regimes. Each returned slightly different results for the Myrmeleontiformia—some placed Nymphidae as sister to the AMC, some Nemopteridae, but all placed Ascalaphidae and Myrmeleontidae together. A few of the analyses suggested the Ascalaphidae are paraphyletic with respect to Myrmelontidae. However, taxon sampling of the two families was rather small—only two species each of Myrmeleontidae and Ascalaphidae were sampled. Of the Myrmeleontidae, though, both are putatively basal lineages, the aforementioned *Stilbopteryx* and *Palpares*. The Ascalaphidae were represented by two split-eyed genera, *Ululodes* and *Libelloides*.

The only previous author to have focused attention on phylogeny within the family Ascalaphidae was Henry (1978a, 1978b). He presented a simple phylogeny (1978b, Fig.

2) that optimized several characters: (i) evolution and loss of repagula ("barriers": defined as abortive eggs laid below egg masses on twigs in some owlflies), from abortive eggs with trophic functions to abortive eggs with barrier function to ant-repelling repagula, and then lost; (ii) split eyes; and (iii) ovariole number. His phylogeny proposed one clade containing *Ascalobyas* (as *Byas*), *Haploglenius* (as *Haploglenius* and *Verticillecerus*—see Chapter 3), and *Amoea*; one for *Episperches* (now *Amoea*) judged as transitional, one for the Ululodini, and one for the Old World split-eyed tribes Suhpalacsini, Acmonotini, Proctarrelabrini, Hybrisini, Encyoposini, and Ascalaphini. Thirteen unnamed Old World genera were placed tentatively at the base of the tree. Hypotheses of phylogenetic relationships based on morphological data have also been presented in chapters 1–3 for the genera *Allocormodes* McLachlan and *Tmesibasis* McLachlan, and for the New World Haplogleniinae.

Currently (Tjeder 1992) the family Ascalaphidae comprises three subfamilies: the Albardiinae, already discussed, with a single species from Brazil; the Haplogleniinae, or "entire-eyed owlflies", with ca. 100 valid species in 24 genera distributed in North and South America, western Asia, Africa and Madagascar; and the Ascalaphinae, or "split-eye owlflies", with approximately 350 described species in nearly 75 genera, found worldwide. The Haplogleniinae are diagnosed by having antennae that reach past the halfway point between the forewing base and the pterostigma (as opposed to the short antennae of Albardiinae which do not), and that lack a transverse furrow across the eyes.

The Ascalaphinae, conversely, are diagnosed by equally long antennae and the presence of a transverse sulcus-like division across the eye.

The monophyly of the two large subfamilies has been assumed based on the feature of the eye. However, the Haplogleniinae, which express entire eyes, are not, in fact, united by a shared derived feature, but rather a shared plesiomorphy. Further, several taxa in both families express intermediate states of eye division. For example, Tjeder (1992) placed his African genus *Proctolyra* in Haplogleniinae because its eyes, though divided, are only weakly so—the furrow is not deep or sulcus-like. However, he acknowledged it possesses other features that suggest it belongs within the Ascalaphinae: well-developed male ectoprocts, seen otherwise only in the Ascalaphinae, and the presence of the pleurostoma. Nevertheless, he interpreted the division of the eye to be of such importance as to outweigh those other features in determining taxonomic relationships, and for that reason placed *Proctolyra* in its own tribe, Proctolyrini, interpreting it as a "missing link" between the subfamilies. The strange South American genus *Fillus* also has equally very weakly divided eyes, but was placed in the Ascalaphinae by Navás (1919), chiefly on account of its wing venation, which is similar to Old World species in the tribe Suhpalacsini, but also the presence of the abdominal tergal process of males seen in other Ascalaphinae. In Chapters 2 and 3, the eyes of several species of Old and New World Haplogleniinae—*Tmesibasis*, *Ascalobyas* and *Neascalobyas*—were described as expressing a very slight posteromesal depression suggestive of an incipient and possibly progressive division. Thus, the reliability of the eye division as an indicator of phylogeny is not at all certain; split eyes may have arisen multiple times within the owlflies.

Tribal classification within the Ascalaphidae is even more problematic. Though a few of the tribes are based on what appear to be reliable characters, several are diagnosed primarily by combinations of plesiomorphic or convergent features, are described with insufficient detail to enable a proper tribe-level identification for many species, and, geographically-speaking, seem implausible. Identification of species to tribe is also confounded by the fact that several of the tribes are determined solely by the expression of male morphology. Suhpalacsini van der Weele, as one example, is diagnosed by the males having more or less undeveloped ectoprocts (a plesiomorphic feature) and sometimes bearing a swelling or process on some part of the abdominal tergum (a derived feature). In the South American suhpalacsine genus *Fillus*, an acuminate process arises from fused T1 plates; but in the Australian *Megacmonotus* New and *Pictacsa* New, a stout projection rises from T2; and in many suhpalacsine genera, no projection occurs at all. As another example, *Neohaploglenius* Penny, *Verticillecerus* van der Weele and *Ascaloptynx* Banks have been placed in Verticillecerini Orfila (Penny 1982a), separated from other New World Haplogleniinae on the basis of the forewing being proximally narrow and the anal angle developed into a process. But as discussed in chapters 1–3, wing narrowing is common and convergent across the Ascalaphidae and varies even within genera (including these genera—see chapter 3), and thus by itself is not necessarily a good indicator of phylogenetic relationships, and cladistic evidence was recently found to sink these genera into *Haploglenius* Burmeister with other species not expressing extreme wing narrowing (see chapter 3).

More on tribes of Ascalaphidae

A comprehensive tribal structure for the Ascalaphidae was first proposed by van der Weele (1909). Current tribal concepts are fundamentally the same but with a few important changes.

Van der Weele proposed no tribes for the Haplogleniine (as "Holophthalminae"). For the Ascalaphinae (as "Schizophthalminae") he proposed seven tribes. They are characterized below according to his fundamental concepts, but with characters modified to reflect current names of structures.

<u>Acmonotini</u>: Mp_2 fork distinct, Mp_{2p} joining short Cua; antennae without basal verticils; male ectoprocts not produced; T2 of ♂ with special outgrowth.

<u>Ascalaphini</u>: Mp_2 fork distinct, Mp_{2p} joining short Cua; antennae without basal verticils; male ectoprocts produced; T2 of ♂ without special outgrowth. Antennae of ♂ straight in basal half. S9 large in relation to ectoprocts.

<u>Encyoposini</u>: Mp_2 fork distinct, Mp_{2p} joining short Cua; antennae without basal verticils; male ectoprocts produced; T2 of ♂ without special outgrowth. Antennae of ♂ straight in basal half. S9 small in relation to ectoprocts. Pterostigma short, with few crossveins.

Hybrisini: Mp_2 fork distinct, Mp_{2p} joining short Cua; antennae without basal verticils; male ectoprocts produced; T2 of ♂ without special outgrowth. Antennae of ♂ curved in basal half. S9 large in relation to ectoprocts. Pterostigma long, with many crossveins.

Proctarrelabrini: Mp_2 fork distinct, Mp_{2p} joining short Cua; antennae with basal verticils; male ectoprocts produced; T2 of ♂ without special outgrowth.

Suhpalacsini: Mp_2 fork distinct, Mp_{2p} joining short Cua; antennae without basal verticils; male ectoprocts not produced; T2 of ♂ without special outgrowth.

Ululodini: Mp_2 fork indistinct, Cua long, sinuous; antennae without basal verticils; male ectoprocts not produced; T2 of ♂ without special outgrowth.

Navás (1912) modified the concept of Acmonotini to include males with processes on the third tergite, and moved *Stylonotus* Needham (now *Stylascalaphus* Sziráki) into it. Soon after (1919), he sunk the tribe into Suhpalacsini and modified the concept of the latter to include males with tergal processes on the first, second, or third tergite. He did so because he realized his new species *brethesi*, which he placed in his new genus *Fillus* and in which males have the process on the first tergite, was congeneric with Van der Weele's (1909) *Acmonotus paradoxus*. Van der Weele had described *paradoxus* from a single female, not knowing anything about the tergum of the male. Navas (1919) also included a key to the species he included in Suhpalacsini. Navás's refined Suhpalacsini may be characterized as follows:

Suhpalacsini (=Acmonotini): Mp_2 fork distinct, Mp_{2p} joining short Cua; antennae without verticils; male ectoprocts sometimes slightly produced; T1, T2 or T3of ♂ sometimes with a special outgrowth.

New (1984) was slightly ambiguous as to his position regarding tribal placements for the Australian genera in his revision of the Australian owlflies, but he seems to have tentatively accepted Navás's definition for the Suhpalacsini and retained the Australian fauna within it until a future revision of tribes within the Ascalaphidae could be performed.

Tjeder (1972) revised the type concept of the genus *Ascalaphus* and moved most of its species to *Libelloides* Schäffer. But he made no comment concerning tribal placements. In 1992 his mostly complete revisions of the African owlflies were published posthumously. In them he reinterpreted Ascalaphini to include only genera whose males have the ectoprocts undeveloped, which corresponds, in part, with van der Weele's original definition of Suhpalacsini before its modification by Navás (1919). He did not address tribal placement for *Libelloides* species formally placed in Ascalaphini, nor for related genera also formerly placed in Ascalaphini, which, as a result, no longer fit. In his revision the new tribe Ululomyiini was also created to contain the new genus *Ululomyia*, in which the males have well-developed lyrate ectoprocts.

Tribes within the Haplogleniinae were first proposed by Orfila, who created Verticillecerini to contain species in which the forewing base is narrowed and the axillary angle produced into a process. Penny (1982a) followed Orfila and placed into Verticillecerini *Verticillecerus* van der Weele, *Neohaploglenius* Penny and *Ascaloptynx* Banks. Penny then used the name Haplogleniini Newman to contain the remaining members of the New World Haplogleniinae, in which he interpreted the forewing base to not be narrowed, and the axillary angle not produced.

Tjeder (1992) created new tribes for the African and Malagasy Haplogleniinae. Most of the African genera he placed in Melambrotini, but he created four monobasic tribes to contain what he considered to be distinctly independent lineages: Allocormodini, Campylophlebiini, Proctolyrini, and Tmesibasini.

The present study

This study builds on that of Winterton et al. (2010) by presenting the first large-scale phylogenetic hypothesis for the family Ascalaphidae based on morphological and molecular data. Here are presented combined analyses of 25 morphological characters and three genes, 16S, 18S, and cytochrome oxidase I (COI), for 77 species from all five currently recognized extant myrmeleontiform families, in order to evaluate monophyly at three primary taxonomic ranks: family, subfamily and tribe. Three phylogenetic paradigms were employed to explore relationships: parsimony, maximum likelihood, and Bayesian inference. In addition, evolution of the eye (entire vs. divided) and the pleurostoma, the latter a feature suggested by Tjeder (1992) as possibly useful for diagnosis of the Ascalaphinae, are briefly discussed.

Materials and methods

Taxon sampling

Seventy-six species from the five families of Myrmeleontiformia (Psychopsidae, Nymphidae, Nemopteridae, Myrmeleontidae, Ascalaphidae) were chosen for analysis (Table 2). Sampling was deepest for Ascalaphidae and Myrmeleontidae. Efforts were made to sample as thoroughly as possible from the Ascalaphidae. Two of three subfamilies were sampled (extractions of *Albardia* from dry pinned specimens and older specimens in 70% EtOH were attempted but no DNA was recovered). Of Haplogleniinae, 11/24 genera and 3 *Haploglenius* species groups in 5/7 tribes (Allocormodini, Haplogleniini, Melambrotini, Tmesibasini, Verticillecerini) were sampled (extractions of Campylophlebiini [*Campylophlebia* McLachlan] and Proctolyrini [*Proctolyra* Tjeder] from dry pinned specimens were attempted, but no DNA was recovered). Of Ascalaphinae, 13/75 genera in 6/7 tribes (Ascalaphini, Hybrisini, Proctarrelabrini, Suhpalacsini (Acmonotini), Ululodini, Ululomyiini) were sampled (extractions of Encyoposini were attempted from dry pinned specimens, but no DNA was recovered). In the Myrmeleontidae, representation was obtained for each of the subfamilies (Myrmeleontinae, Palparinae, Stilbopteryginae). In the Myrmeleontinae, sampling included the tribes Acanthaclisini, Brachynemurini, Dendroleontini (subtribes Dendroleontina and Periclystina), Myrmeleontini (subtribe Myrmeleontina), and Nemoleontini (subtribe Nemoleontina). In the Psychopsidae only a single exemplar was successfully amplified. In Nymphidae four species in two genera were sampled. In Nemopteridae, two species were successfully amplified, but the sequence of one exhibited anomalous properties during analysis and was removed. Included in taxon sampling for Ascalaphidae are three species whose information was extracted from GenBank. In total, including the outgroup, 77 species were sampled, including the outgroup *Polystoechotes*.

As outgroup, *Polystoechotes* Burmeister was selected. In Winterton et al. (2010) a clade containing Ithonidae+Polystoechotidae (total evidence parsimony analysis)—this sometimes allied with Hemerobiidae+Chrysopidae (morphology, Bayesian analyses)—was consistently placed as sister group to the Myrmeleontiformia.

Morphological characters

Twenty five anatomical characters were coded for all exemplars included in this study (Table 3). Characters were selected that have been established in the literature or observed during direct studies to consistently indicate shared relationships for higher-level groupings, in particular for the Ascalaphidae, but also across the Myrmeleontiformia.

Adult

Head

1. Paraocular band: 0, absent; 1, present, well-formed.

Within the Myrmeleontiformia, the paraocular band (see Chapter 1) first appears in Nymphidae, and is a well-formed feature in *Stilbopteryx*, *Albardia* and Ascalaphidae.

2. Extra-torular sclerites: 0, absent, or narrow, weakly formed, widely separated and not mesally fused; 1, present, well-formed, mesally fused.

These sclerites (see Chapter 1) first begin to be well-formed in some antlions, and are well-developed in *Vella*, Palparinae, Stilbopteryginae and Ascalaphidae.

3. Prefrons: 0, absent; 1, present, well-formed.

Tjeder (1992: p. 15) first used this term to delineate in owlflies the dorsal portion of the frons on which the antennae are mounted (see Chapter 1, A1 Figs. 001, 002); this area or plate is deeply angled into the head such that the antennae, which arise from the toruli, are directed dorsally on the head.

4. Anterior tentorial pit shape: 0, opening round, or slit-like but short (with length approximately coequal to that in species with pit round); 1, opening oblong, slit-like but long (at least two to three times longer than width of pit in specimens with pit round).

The true shape of the pit is easiest to see in macerated specimens. It is essentially round or dorsoventrally rather short in most Myrmeleontiformia but becomes elongate in antlions and owlflies and helps defined the mesal margin between the paraocular band and the frons.

5. Pleurostoma: 0, absent; 1, present.

Tjeder (1992), from his examinations of numerous Ascalaphidae species, postulated this small facial sclerite might be a synapomorphy for the Ascalaphinae, but in the present study it was discovered in the genera *Idricerus* McLachlan, *Nicerus* Navás (both not included in analysis), and *Protidricerus* van der Weele.

6. Labial palpus distal segment: 0, not swollen subapically, or only slightly enlarged at sensory pit, not elongate; 1, substantially swollen subapically at sensory pit, not elongate; 2, swollen apically, extremely elongate.

Swollen terminal palpimeres occur in Myrmeleontidae and *Nymphes*.

Antennae

7. Antennae length: 0, less than half forewing length in spread specimens; 1, longer than half forewing length in spread specimens.

All Ascalaphidae (except *Albardia*, not included) express some degree of antennal prolongation, and most have the antennae longer than half the forewing length.

8. Antennal apex form: 0, filiform (without a distinct club), antennomeres at apex as long as or shorter than wide; 1, clavate, with antennomeres in mesal portion of "club" much shorter than wide; 2, capitate, with antennomores in mesal portion of "club" *much shorter than wide; 3, elongate spindle-shaped, with antennomores in mesal portion of "club" longer than wide.*

Antlions and owlflies are generally characterized equally as having "clubbed" antennae, but the expression of the club is quite different between the two families. In Ascalaphidae and Stilbopteryginae the antennomeres comprising the club are fewer and broaden quickly near the club base, giving the club a more capitate appearance, whereas in most antlions and some other Myrmeleontiformia they are numerous and broaden gradually throughout the basal half of the club, giving the club a more clavate appearance. In several species of *Tmesibasis* the club is very narrow and difficult to distinguish, and the antennomeres comprising it elongate (see Chapter 2).

Eyes

9. Eye shape: 0, entire, sometimes a posteromesal depression present, round, ocular diaphragm in one plane or slightly curved; 1, divided into upper and lower lobes by a deep sulcus–like depression or invagination, both parts together at least slightly oblong, with ocular diaphragm bent, in two planes.

Most Myrmeleontiformia have the eyes round and entire, but the Ascalaphinae are diagnosed by expressing a "divided" eye. Nearly all authors have characterized the division as present or absent, but in actuality, it varies highly in its expression from genus to genus. For example, in some genera, including within the Haplogleniinae, the division is present but very slight and/or incomplete (*Fillus* [Ascalaphinae], *Ascalobyas*, *Proctolyra*, *Tmesibasis* [latter three Haplogleniinae]); in other genera (all Ascalaphinae) it is expressed in an intermediate state (e/.g., *Megacmonotus*); whereas in others still (all Ascalaphinae) it is quite distinct (*Bubopsis*, *Libelloides*, *Ululodes*). In some genera the divide is merely a shallow furrow, whereas in others the upper portion appears so distinct as if were nearly an entire second eye placed on top of the first, and is distinctly superpositional. In some the furrow between the two parts is a rather straight line, while in others it is distinctly curved. The eye also varies in its degree of oblongation, both antero-posteriorly and dorsoventrally. It also varies in the ratio of the size of the ventral portion to that of the dorsal portion, with some species actually showing slight increased size in the ventral portion, although the reverse is more often true. The shape of the ocular diaphragm is also useful in determining the degree of division—those species with very well-expressed divisions often have the diaphragm distinctly curved or bent into two planes. This bend may or may not correlate with the depth and curvature of the external furrow in other species. In spite of these many differences, it is useful to include the eye division as a character here in order to test if it corresponds with currently interpreted notions of phylogeny.

Thorax

10. Pronotum length: 0, more than half width, often nearly as long as broad; 1, less than half width, collar-like.

Short pronota are characteristic of the Ascalaphidae, Albardiinae and Stilbopteryginae.

11. Prothoracic valve, males: 0, undeveloped; 1, produced, developed.

This is a feature well-developed in *Ascalobyas*, *Neascalobyas*, and many *Haploglenius*. It also appears, curiously, in *Fillus* (not included).

12. Mesoacrotergite, males: 0, entire; 1, medially emarginated.

The medially emarginate mesoacrotergite is shared by a few species of *Haploglenius*.

13. Pleural pattern: 0, absent, variegated, indistinct; 1, single yellow longitudinal stripe; 2, paired yellow oblique stripes; 3, posteriorly yellow, anteriorly black; 4, almost entirely black, anteriorly with a yellow maculation; 5, in dorsal half black, in ventral half orange.

Distinct pleural patterns defined *Haploglenius* spp., and appear to be useful in aggregating *Libelloides* and some *Suphalomitus*.

Legs

14. Metathoracic tibia to tarsus ratio: 0, > 1.2; 1, < 1.1.

In owlflies and many antlions the tibia are rather short and the tarsi relatively quite prolonged such that they are approximately coequal. This is most readily evaluated among the families by examining the hind legs, which are generally distinctly longer in non-owlfly Myrmeleontiformia.

Wings

15. Relative length: 0, fore-and hind wing at least somewhat proximal to one another in length; 1, hind wing considerably longer than forewing, usually several times as long.

Very long hind wings are a distinctive feature of Nemopteridae.

16. Recurrent vein: 0, present; 1, absent.

Relative to Myrmeleontiformia, this is a primitive feature. It was included to orient the Myrmeleontiformia to the outgroup. The vein occurs in Psychopsidae and Nymphidae.

17. Hypostigmatic cell: 0, present; 1, absent.

The cell subtending R near the stigma is elongate in all Myrmeleontiformia except Ascalaphidae.

18. Sc, R and Rs terminal anastomosis: 0, absent; 1, present.

Oswald (1993: 41) disassembled the cohesiveness of the so-called "vena triplica", indicating it should be re-characterized as a set of concurrent spatial features occurring in many taxa and not necessarily unique in Psychopsidae. One portion of the feature that does seem to be unique to the family, based on his description, is the terminal anastomosis of the veins. This character was coded here as a synapomorphy for Psychopsidae.

19. Marginal forking of veins along distal part of hind margin: 0, 10 furca or greater; 1, 7 furca or fewer.

Reduction in the furcation of marginal veins is a distinct attribute of Ascalaphidae.

20. HW Cua distal trace: 0, absent; 1, present, continuing past Mp_{2p}, long and usually curved.

McLachlan (1871) and van der Weele (1909) both emphasized the sinuous form of the "postcosta" (Cua) of the HW, and van der Weele used it as a diagnostic feature to set apart his tribe Ululodini. The feature also occurs in *Stilbopteryginae* and *Albardia*, and van der Weele and others have suggested its presence indicates a close relationship between them and the Ululodini.

21. Pilulla axillaris (Eltringham organ), males: 0, absent; 1, present.

This swelling at the axillary margin of the HW in males occurs in Myrmeleontidae and may be a synapomorphy for the family. It was observed by McLachlan and others to occur in *Stilbopteryx*, and supported their view that the genus is more closely related to antlions than to owlflies.

Abdomen

22. Position of segment 8 spiracle opening, females: 0, on T8 [some Libelloides]; 1, on pleural membrane [Ululodini].

In most Myrmeleontiformia and Ascalaphidae, the spiracle is positioned on the ventrolateral reaches of T8. In Ululodini, it occurs on the pleural membrane. This phenomenon was observed by N. Penny (pers. comm.) and proposed as a possible synapomorphy for the genus. In this study it was observed in every ululodine examined, and may, in fact, be a synapomorphy for the tribe.

23. Pleuritocavae, hind margins of abdominal pleura 7 and 8, males: 0, absent; 1, present.

Pleuritocavae occur in many Neuropterida (see Tjeder 1992: 30 for a brief discussion). Within the Myrmeleontiformia, they are expressed most dramatically in several species of *Haploglenius*.

Larvae

24. Metathoracic tibia + tarsus: 0, separate: 1, fused.

Fusion of the hind tibia and tarsus, described briefly by Withycombe (1924: 325) unites the Myrmeleontidae and Ascalaphidae (New 1982; Badano & Pantaleoni 2014).

25. Scolus-like processes: 0, absent; 1, present.

Notes: Badano (2014: 288) renamed the feature commonly referred to as scoli (singular='scolus') by numerous authors (e.g., MacLeod 1970; Henry 1976, 1978a, 1978b; Tjeder 1992) "scolus-like process", on the grounds that they are not homologous with true scoli, which were named originally for Lepidoptera and later for Coccinellidae.

Gene selection, DNA extraction, amplifications, and gene sequencing

Because of their utility in previous Neuropterida-targeted phylogenetic studies (Haring and Aspöck 2004, Winterton et al. 2010), the mitochondrial genes cytochrome oxidase subunit I (COI) and 16rRNA (16S), and the nuclear genes 18SrRNA (18S), and carbamoyl-phosphate synthetase-aspartate transcarbamoylase-dihydroorotase (CAD) were selected for use in this study.

The majority of exemplar material included for this project was freshly caught during fieldwork by the author and associates and was stored in 80–100% ethanol -80°C; a small percentage of donations and loans arrived stored in ethanol of lower quality (~70%). DNA extraction of all these specimens was performed using the Quiagen DNeasy® blood and tissue kit (Qiagen, Germantown, MD), following manufacturer's instructions for animal tissues. The remaining exemplars used were pinned museum specimens. For this group, an additional step was added to the beginning of the extraction process. A single hind leg was carefully removed from a specimen at the coxal joint using sterilized needlepoint forceps. It was then placed in a sterile vial containing 95% ethanol to soak for several hours or overnight. Following this step the leg was then briefly sonicated to remove loose particles, carefully washed again in 95% ethanol, and placed in a sterile vial containing 1X PBS (phosphate buffered saline) and allowed to soak for a second night. The next day the leg was removed and placed in a sterile weight boat. Using a sterilized razor blade, small incisions were made on the ventral surfaces of the femur and tibia. The PBS solution was then poured or pipetted off to remove most residues. The leg was then walked through standard extraction formulae. Care was taken in the process to not excessively damage the leg, and following the first centrifuge step the leg was carefully removed from the spin column, washed again, and returned to the source specimen from which it came.

Early PCR tests were conducted with small subsets of freshly collected ingroup taxa to determine which gene regions might amplify well with published primers. Amplifications were successful for 16S, COI domain 2, and 18S domain 1; they were partially successful for 18S domains 2 and 3, and CAD. Subsequent evaluations of 18S domain 2 PCR products via electrophoresis revealed frequent but inconsistently-expressed high length variability suggestive of potentially very long and problematic indel regions, and so the domain was removed from further attempts at amplification. Domain 3 continued to present only mixed amplification success, despite efforts to optimize thermocycling profiles and other procedural variables, and so also was cut. An intensive effort was made to amplify CAD for all major regions (4300+bp) using a two-stage external-internal-primer amplification procedure employed by Winterton et al. (2010, pers. comm.), but this yielded PCR product for only small numbers of taxa, and so the gene, region by region, was ultimately completely eliminated from analysis.

Oligonucleotide primers used in this study are listed in Table 4. Primers for CAD (not reported here) are given in Winterton 2010. Gene regions amplified are reported by taxon in Table 2. For PCR, two commercial master mix solutions were used: EmeraldAmp® MAX PCR Master Mix (Clontech Laboratories, Inc., Mountain View, CA), which operates at a standard extension temperature of 72°C, and 5 PRIME HotMasterMix (5 PRIME, Gaithersburg, MD), which extends at 65°C. PCR protocols used, including novel ‘touchdown’ and other thermocycling regimes optimized for this project, are reported in Table 5.

Amplification of PCR product was confirmed via gel electrophoresis. DNA yields were verified after initial amplifications with a Thermo Scientific NanoDrop Fluorospectrometer (NanoDrop products, Wilmington, DE). PCR product was cleaned with USB® ExoSAP-IT® PCR Product Cleanup (Affymetrix, Santa Clara, CA) following manufacturer's directions.

Sequencing was outsourced to the University of Arizona Genetics Core (UAGC), Tucson, AZ.

Alignment

Chromatogram files were edited using Sequencher™ 4.8 (GeneCodes Corp., Ann Arbor, MI). Verification of the COI alignment was determined in Sequencher by visually checking the open reading frame graphic presented in the contig windows to insure stop codons were not present. A second check was performed in Mesquite (Maddison and Maddison 2011) by coloring nucleotides by amino acid, shifting the reading frame to minimize stop codons (matrix / alter/transform / shift to minimize stop codons), and then manually scanning the matrix for stop codons. A single codon insert of the amino acid leucine (CTA) was detected in *Palpares libelluloides* and *Cordulecerus inquinatus* commencing at site 837. While viewing the COI alignment, it was observed that changes were occurring across the entire dataset at nearly every third position and many first positions. To check for possible saturation, a list of uncorrected P and then general time reversible (GTR) distances were generated in PAUP* (Swofford 2002) and these were plotted against one another in Microsoft Excel 2007 (see Figure 3). The resulting saturation curve revealed the distances forming nearly a straight line, and the line having a high R^2 value (0.9948). Saturation is interpreted to be minimal.

Alignment of the ribosomal genes was carried out in MAFFT (Multiple Alignment using Fast Fourier Transform: Katoh et al. 2005) and GBlocks (Castresana 2000). Following manual alignment, files were exported from Sequencher with gaps removed. These were uploaded into MAFFT on XSEDE at the CIPRES (Cyberinfrastructure for Phylogenetic Research) portal (Miller et al. 2010) and processed using the following settings: 'configure...from scratch (--mafft)'; L-INS-i; distance metric: genafpair (with all defaults); number of cycles of iterative refinement: 1000. During manual alignment 18S was observed to express several indel regions with large suites of gaps. For this reason L-INS-i was chosen because of its ability to better handle region with high variability in length and identity; genafpair was also selected as the best metric for the rRNA datasets because it is optimized for treating large internal gaps. Output files were processed in GBlocks using the web-based utility (http://molevol.cmima.csic.es/castresana/Gblocks_server.html, last accessed July 21, 2014), and the following settings: allow smaller final blocks, yes; allow gap positions within the final blocks, yes; allow less strict flanking positions, no; do not allow many contiguous nonconserved positions, yes. This recipe was understood to be a very conservative model of block selection, but it was favored because (i) in addition to large indel regions present in the manual alignment, several short indel regions for both genes were observed; and (ii) visual evaluation of bases at flanking positions did not instill great confidence in their homology. These settings were determined after performing a set of tests with both the 16S and 18S datasets to evaluate which approaches resulted in the greatest base retention but also the tightest sequences alignments (fewest gaps).

Model selection

For the COI partition, model fit was explored in Partitionfinder (Lanfear et al. 2012), using the following settings: branchlengths: 'linked'; models: 'all'; datatype: 'DNA'; model_selection: 'bic'; search: 'user'. Partitionfinder gave the following results for unpartitioned, and first, second, and third position subpartitions: combined: GTR+I+G; COI 1: GTR+G; COI 2: GTR+I+G; COI 3: TVM+I+G.

Selection of models for the ribosomal genes was performed in JModelTest2 (Darriba et al. 2012; Guindon and Gascuel 2003). For 18S, the following setting were used: candidate models = 88; number of substitution schemes = 11; including models with equal/unequal base frequencies (+F); including models with/without a proportion of invariable sites (+I); including models with/without rate variation among sites (+G) (nCat = 4); optimized free parameters (K) = substitution parameters + 141 branch lengths; base tree for likelihood calculations = fixed BIONJ-JC tree topology. A second test was performed using an ML tree as the base tree for likelihood calculations, and tree topology search operation = NNI. The same procedure was performed for 16S, with all the same settings, except optimized free parameters (K) = substitution parameters + 157 branch lengths. For both the model and NJ/JC optimized analyses of the 18S partition, JModelTest2 selected TVM+I+G. For 16S, both approaches yielded the model GTR+I+G.

Phylogenetic analyses

Parsimony analysis was conducted on (i) the morphological partition and (ii) the total evidence dataset containing the morphological partition + all molecular partitions. Both datasets were analyzed in TNT (Goloboff et al. 2008) using New Technology (NT) searches with the Sectorial search, Ratchet, Tree-drift and Tree-fusing algorithms all employed under default settings. No characters were designated as additive, although the putative plesiomorphic state was coded as 0 and derived states as 1, 2, etc. The consistency index (C. I.) and retention index (R. I.) were generated using the 'stats.run' found at http://tnt.insectmuseum.org/index.php/Scripts. Bremer supports (Bremer 1994) were calculated within TNT using the internal utility.

Maximum likelihood analysis of the molecular datasets was performed in the RAxML-HPC Black Box environment (Stamatakis 1914) at the CIPRES portal (Miller et al. 2010), under the following settings: outgroup: *Polystoechotes*; estimate proportion of invariable sites (GTRGAMMA + I): no; find best tree using maximum likelihood search:

yes; let RAxML halt bootstrapping automatically: yes; print branch lengths: yes. This algorithm was run using four separate partitioning schemes (see Table 6).

RAxML Black Box, however, does not allow the user to designate separate models for different partitions, but instead chooses the best model per partition for the user (when the option is checked). For the four partitions RAxML returned the same result for all subpartitions, as follows: (i) GTR; (ii) subpartitions 0, 1, and 2, all GTR; (iii) partitions 0, 1, 2, 3, and 4, all GTR; (iv) partitions 0, 1, 2, and 3, all GTR.

Bayesian analysis was performed in MrBayes 3.2.2 (Ronquist and Huelsenbeck 2003) on XSEDE at the CIPRES portal (Miller et al. 2010). The analysis was run for 10 million generations. Stationarity was determined to occur after approximately 535,000 generations (via examination of average standard deviations of split frequencies), and the first 1 million generations were discarded as burnin (see Fig. 4). The harmonic mean of all runs was -32254.75; the harmonic mean with burnin runs discarded was -29044.45. Total potential scale reduction factor (PSRF) for all parameters after burnin discard was 0.9999806.

Results

Morphological data phylogeny

Analysis of the morphological data partition by itself resulted in six equally parsimonious trees.

A strict consensus cladogram of these trees can be seen in Fig. 5. This cladogram is largely unresolved, particularly at the genus and species levels. It presents its strongest signal at the node containing Myrmeleontidae + Ascalaphidae (Bremer support: 3), and places representatives of the myrmeleontiform families as stem lineages leading up to the Ascalaphidae. The lack of species-level resolution is to be expected—very few characters were coded in the morphology dataset that address relationships within the families.

Molecular data phylogeny

Four trees were returned from RAxML analyses of the molecular data, one for each partition scheme. The trees are not identical but are all quite similar to one another, differing primarily in the placement of the genus *Protidricerus* within the Ascalalaphidae from the partitioned analyses to the un-partitioned analysis, and in the arrangement of tribes within the Myrmeleontidae, which experienced some internal rearrangements in the various analyses. Fig. 6 presents a phylogram of the un-partitioned result (partition 'i'). The tree is color coded to reflect family-level relationships as they are currently defined. This topology illustrates a trend seen in the results of all analytical approaches—strong support for some medium and lower-level groupings, including species and genus groups and several tribes, but somewhat questionable placements and thus taxonomic uncertainty at higher levels within the Myrmeleontiformia and Ascalaphidae. In this case, the tribe Ululodini is placed separately from remaining Ascalaphidae as sister group to a paraphyletic assemblage of myrmeleontid groups + remaining Ascalaphidae, which are monophyletic.

Some of the well-supported mid- and lower-level taxonomic groups include the Ululodini (bootstrap: 100), Palparinae (bootstrap: 99), Stilbopteryginae (bootstrap: 100), New World Haplogleniinae (NWH)(bootstrap: 87), African Haplogleniinae (bootstrap: 88), Australian Suhpalacsini (bootstrap: 94), and *Libelloides* (bootstrap: 100). These relationships were recovered in every analysis (including Bayesian and parsimony; see below) with high support.

Other phenomena can be observed in this figure that are also consistently reflected in other topologies. The arrangement of families is constant across the different analytical approaches (see below): Psychopsidae is always placed at the base of the Myrmeleontiformia; Nymphidae is always next, and then Nemopteridae, which is always placed as sister to the AMC. One consistent message from the data in this paper is that the arrangement of families within the Myrmelentoformia takes the form Psychopsidae + (Nymphidae + (Nemopteridae + (Myrmeleontidae + Ascalaphidae))).

Total evidence analysis: Bayesian phylogeny

Bayesian analysis (Fig 7) placed the Ascalaphidae as monophyletic with 100% posterior probability support. The Ululodini were placed at the base of the family, separate from other split-eyed species. Myrmeleontidae were once again recovered as paraphyletic. The Stilbopteryginae were placed as sister to the owlflies and near the base of the antlions, an hypothesis put forward by van der Weele (1909) and Tillyard (in Hacker 1913). They were also placed immediately distad of the Palparinae (a close relationship between the two subfamilies was proposed by Kimmins 1940). Within the Ascalaphidae, the Ululodini were placed as sister to all remaining species, with high support (pp=100%). African Haplogleniinae were then placed as sister to the remaining ascalaphid species, also with high support (pp=100%). The NWH were once again monophyletic with high support (pp=100%), although their inner relationships are somewhat unresolved. In the remaining Ascalaphidae, the entire-eyed *Protidricerus* is placed in a small clade with the split-eyed *Proctarrelabis* and one species of *Suphalomitus* with rather high support (pp=88%). Together they form the sister group to the remaining owlflies, which are all split-eyed. Relationships within the large split-eyed owlfly clade differ slightly from the ML topology, mainly in the positions of

Protidricerus, the small clade (2 spp.) containing *Proctarrelabis*, and the clade (5 spp.) containing *Suhpalacsa princeps*.

Total evidence analysis: Parsimony phylogeny

Analysis in TNT resulted in two equally parsimonious trees with a length of 6701. One of the trees placed Stilbopteryginae + Palparinae as sister to the African Haplogleniinae, but the other tree (Fig. 8) expressed most of the same relationships as the ML and Bayesian topologies. The RI and CI for the topology are 0.528 and 0.235, respectively.

As in the Bayesian tree, Ascalaphidae were recovered as monophyletic, with the Ululodini placed at the base of the owlfly clade. Support for this relationship, however, was very low (Bremer: 1). Bremer support for the Ululodini was 15. The NWH were placed as sister to the remaining Ascalaphidae (as in the ML analysis), but with low support (Bremer: 1). Within this clade, the African Haplogleniinae were placed as sister to the remaining species, but again with low support (Bremer: 1). Monophyly of the NWH had a support value of 4, and support for the African Haplogleniinae was 5. The remaining Ascalaphidae were strongly supported as monophyletic with a Bremer support value of 10. Within this group, the Australian Suhpalacsini and Libelloides were both supported as monophyletic, each with Bremer supports of 10.

The Myrmeleontidae were nearly recovered as monophyletic, with only the Dendroleontini placed outside on the stem leading basally toward Nemopteridae. This differed from other analyses (see Figs. 6, 7). Within Myrmeleontidae, Palparinae (Bremer: 9) and Stilbopteryginae (Bremer: 28) were placed together with a support value of 6. Support values for other basal nodes ranged from 1 to 4.

Although branch lengths of stem lineages along the backbone of the tree were somewhat short and expressed weak support, the analysis was able to recover a monophyletic Ascalaphidae (unlike the maximum likelihood analysis). The parsimony topology will now be used to optimize and discuss intrafamilial and tribal relationships and geographic distributions.

Discussion

Subfamilial relationships

Figure 9 displays the total evidence parsimony cladogram with subfamily relationships for the Myrmeleontidae and Ascalaphidae optimized onto it (by color). Within these two families, only the subfamily Albardiinae is not represented. In the Myrmeleontidae, the Palparinae and Stilbopteryginae are each monophyletic and are placed as sister taxa to one another. Together they are placed as sister to a paraphyletic Myrmeleontinae that does not include Dendroleontini. Dendroleontini is instead placed as sister to the remaining Myrmeleontidae + Ascalaphidae. In the other analyses (Figs. 6, 7), Dendroleontini were placed as sister to *Myrmeleon* + *Glenurus*, but within a paraphyletic Myrmeleontinae, rather than outside of it.

The Ascalaphidae in this analysis, at the subfamily level, are broadly paraphyletic. Neither the entire-eyed Haplogleniinae nor the split-eyed Ascalaphinae are monophyletic. The Haplogleniinae, which have long been inferred to represent the most primitive group outside of the Albardiinae, are placed as three well-supported non-sister lineages. The largest two are endemic to the New World and Africa/Madagascar (Fig. 9, triangle and cross, respectively). For these two groups, their non-monophyly is not surprising, as no shared morphological characters that might be interpreted as synapomorphies (aside from entire eyes) have been discovered. The third traditionally haplogleniine lineage, represented in the analysis by the genus *Protidricerus*, is a small group that occurs in Asia, and will be discussed in more detail below.

The Ascalaphinae are divided into two main groups. The larger one has the haplogleniine genus *Protidricerus* imbedded within it (suggesting it belongs within Ascalaphinae—see further discussion in following paragraphs) and includes species from Africa, Asia, Australia and Europe. The smaller clade comprises the exclusively New World tribe Ululodini, placed at the base of all owlflies. The Ululodini, in many regards, are highly derived. Their eyes are distinctly split, more so than in many other Ascalaphinae. Their bodies are small, compact and aerodynamic. *Ululodes* has distinct abdominal patterns, and several *Cordulecerus* species display wings with highly modified shapes and maculation. In addition, the antennae of *Ascalorphne* are greatly elongated. But the Ululodini also retain several plesiomorphic features. In the hind wings the medial triangle has not formed; the Mp^2 fork is not a distinctive feature, and Cua is first sinuous and then continues down the length of the wing, a venational behavior seen in Stilbopteryginae and Albardiinae but no other owlflies. Many ululodines also have the wings unreduced basally. The key attribute, then, pulling them together with other Ascalaphinae, is the split eye. If the divided eye represents a parallelism, rather than a synapomorphy, the basal placement of Ululodini seems reasonable. However, such a consideration leads to the conclusion that the entire traditional classification of the owlflies must then be dismantled. The divided eye, which has served as a lynchpin of owlfly taxonomy for nearly a century and a half, must now be reevaluated and reinterpreted. New characters will need to be sought to diagnose and define newly demonstrable monophyletic groups.

During preparation of the morphology matrix, it was discovered that the pleurostoma is present in the entire-eyed Asian genus *Protidricerus*. This was quite surprising. Tjeder (1992: 60), as a result of his comparative anatomical research on numerous genera of owlflies, reported that the pleurostoma, a small facial sclerite he had recently discovered, occurred in virtually none of the Haplogleniinae and all of the Ascalaphinae that he had examined. Such a statement suggested that the plate might represent a unifying feature for the Ascalaphinae. Tjeder noted one exception, however—his new African genus

Proctolyra (not included in this analysis), which expresses the pleurostoma quite distinctly. Unlike (most) other ascalaphines, *Proctolyra* has the eyes only very weakly divided, and for this reason, Tjeder decided to place it in the Haplogleniinae (in its own tribe). But, along with the pleurostoma, it expresses at least one other distinctly ascalaphine characteristic—the males have exceptionally long and produced ectoprocts. No other haplogleniine expresses strongly produced ectoprocts. Now, it seems, *Proctolyra* is not the only owlfly with an entire (or nearly entire) eye and a pleurostoma. *Protidricerus* also has it.

During examinations of Haplogleniinae genera, the pleurostoma was newly discovered to also be present in the central Asian entire-eyed genera *Idricerus* and *Nicerus*, which were not included in this study. It was not observed in the central Asian haplogleniine *Ptyngidricerus*, however, nor in any other genus of Haplogleniinae, the latter of which have nearly all now been examined.

Protidricerus are medium sized, dark-grayish, entire-eyed owlflies rather broadly distributed in Central and East Asia. Fewer than a dozen species have been described, although they are only known from few specimens, and their true diversity may be much greater. In all analyses in this study they are placed near to the south African genus *Proctarrelabis*, a member of the African tribe Proctarrelabrini diagnosed by having long verticils at the base of the antennae. *Protidricerus* lacks these verticils, but are similar in size, wing shape and in the shape of the cells of the wings. These similarities are slight, however, and cannot necessarily be taken as evidence of strong relatedness. Furthermore, the genitalia of the males are completely different. In *Protidricerus* the ectoprocts are entire and simple, and the ninth sternite small, undeveloped and glabrous, but in *Proctarrelabis* the ectoprocts are greatly produced and complex and the ninth sternite large, robust, and with a mesally produced margin and auxiliary setae.

In light of newfound understanding that the division, or lack thereof, of the owlfly eye can no longer be placed above all other considerations in evaluating taxonomic limits within the Ascalaphidae, it opens the possibility that the large clade of owlflies placed together in the lower reaches of the phylogeny, while not united in all cases by the divided eye, may instead be united by the presence of the pleurostoma. *Idricerus* and *Nicerus*, for example, which express some anatomical similarities to *Protidricerus* in wing shape and venation, may, in fact, belong with it as a branch closely allied to Old World divided-eye owlflies. Further investigations that include them and incorporate more morphological and molecular data will be needed to determine this.

Tribal monophyly

In Fig. 10 terminal taxa are color coded to indicate their tribal placement under current definitions. Within the Ascalaphidae, only the Ululodini are recovered as monophyletic and well-supported (Bremer: 15; see Fig. 8). The New World Verticillecerini and Haplogleniini are each broadly paraphyletic with respect to one another, but together they form a monophyletic clade (Bremer: 4). The Allocormodini and Tmesibasini were placed within the Melambrotini; collectively they form a monophyletic grouping (Bremer: 5). The Suhpalacsini are placed as broadly polyphyletic with regards to other divided-eye owlflies. The Australian fauna, however, were well-supported as monophyletic (Bremer 10—see also Fig. 11). All remaining tribes were paraphyletic. *Deleproctophylla* and *Libelloides*, which formerly were placed in Ascalaphini but which have had no formal tribal placement since Tjeder revised the type concept of *Ascalaphus* (1972) and the tribe Ascalaphini (1992), were not placed together. The phylogeny suggests that some genera are well-supported as sister species or small cohesive generic groups, but these do not correspond with current tribal definitions, nor, necessarily, with what is known about the morphological characteristics of the genera. In *Acheron* and *Ascalohybris*, both Hybrisini, for example, the male ectoprocts are only slightly produced and the ninth sternite is somewhat large but has a simple and more or less entire margin. In *Deleproctophylla*, however, males have greatly elongate and curving ectoprocts (with secondary mesal projections) and the ninth sternite margin is convoluted, being produced mesally and laterally. The fact that these genera were placed together in the parsimony analysis presents a quandary.

Correlation of monophyly to geography

Fig. 11 optimizes geographic distribution onto the parsimony phylogeny. For many clades within the Ascalaphidae it is a better indicator of monophyly than the current generic and tribal-level classification. Speaking in terms of geographic faunas, the Ululodini, New World Haplogleniinae, African/Malagasy Haplogleniinae, and Australian Suhpalacsini are each monophyletic and well-supported. In the future, it may be appropriate to more carefully consider geography in reconstructing tribal classifications, at least for these groups.

Final thoughts and future research

This study represents the first large-scale attempt to determine the phylogeny of the owlflies and the position of the family Ascalaphidae within the Myrmeleontiformia, through the application of modern analytical techniques to morphological and molecular datasets. Evidence presented here confirms that current subfamilial and tribal definitions for the Ascalaphidae are inadequate inthat they place together many tribes and genera into paraphyletic groupings. In particular, the characteristics of the eye alone have been demonstrated as unsuitable for subfamily diagnosis, as they are currently defined (entire vs. divided).

Prior to this study, many authors (Riek 1968, Henry 1978a, Penny 1982a, New 1984, Tjeder 1992) pointed out weaknesses with the current classification and called for revisions of Ascalaphidae and its tribes. The results in this study provide important new clues that should assist in making new placements. Specifically, the Ululodini, New World Haplogleniinae, and African/Malagasy Haplogleniinae have been shown to be monophyletic lineages, and should be regarded as independent taxa in a revised classification. And the remaining owlflies (the non-ululodine Ascalaphinae + *Protidricerus*) appear to be united by the presence of a well-developed pleurostoma, although further comparative anatomical and phylogenetic studies with deeper sampling are needed to confirm this.

Despite these new clarifications, numerous questions remain. Chief among these is the phylogenetic position of several taxa not sampled in this study. These taxa include Proctolyrini and *Fillus*, with their partially divided eyes; and Albardiinae, the putative but unconfirmed basal-most lineage of owlflies. Also in question is the resolution of un- and under-sampled tribes and unplaced genera, each of which calls for deeper taxon sampling. First of these groups are the entire-eyed African tribes Allocormodini, Campylophlebiini, Melambrotini, and Tmesibasini, which should be examined in a phylogenetic framework in coordination with unplaced western Asian entire-eyed genera lacking a pleurostoma (e.g., *Ptyngidricerus*) to test their collective monophyly. Second are the non-ululodine tribes of Ascalaphinae. This latter group appears to be monophyletic (with the addition of *Protidricerus*) and, even with the removal of the Ululodini, collectively still represents the most species-rich single taxon within the family. Each of its sampled tribes (Ascalaphini [sensu Tjeder], Hybrisini, Proctarrelabrini, and Suhpalacsini) was consistently demonstrated here to be broadly paraphyletic, but Encyoposini, as well as many genera in each of the tribes, were not included. The inclusion of these taxa in future studies will further enable improvements to the existing classification of the non-ululodine Ascalaphinae that this study has confirmed are needed.

CHAPTER VI

CONCLUSIONS

Owlflies are beautiful insects. However, the taxonomy and classification of the family have become less accurate and useful since the last monograph (by van der Weele 1909), as the known diversity has mushroomed. This dissertation returns stability to several parts of the family by updating and revising the taxonomy and classification of six genera of Haplogleniinae. At the genus level, one new genus is created and three are sunk, for a net reduction of two genera. In terms of raw numbers of species, this study comprehensively treats ca. 12.5% (58/465) of the known diversity of owlflies. It describes 20 new species, and re-erects five former species-group-name synonyms. It also creates 10 new species-level synonyms. As a result of this work, the net growth of species in the family, after synonymies, is 15 species.

The revisionary chapters of this study greatly improve general knowledge of the treated groups by presenting (i) cladistic analyses, based on extensive morphological data, that provide a robust undergirding for the new infrageneric classifications proposed; (ii) identification keys to all included taxa at all treated ranks (subfamily, genera, species); (iii) comprehensive databases of label data for all examined specimens, including estimated GPS coordinates for all collection sites; (iv) distribution maps for all examined specimens of all species; and (v), extensive illustrations for males and females, where known, of each species.

This dissertation also provides the first robust estimates of phylogeny of the family based on combined morphological and molecular data. These estimates demonstrate that the current classification of the owlflies is paraphyletic at the subfamilial and tribal levels, and that the characters currently used to define them do not constitute unambiguous synapomorphies. A new classification incorporating these and other findings presented herein must be constructed.

A primary aim of this dissertation was to present thorough, useful, and effective methodologies for taxonomic and systematic studies of owlflies that might serve as a templates for future studies. It is the sincere hope of the author that this dissertation opens the door to a career-long exploration into the diversity and wonder of this wonderful family of lacewings.

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APPENDIX 1

1

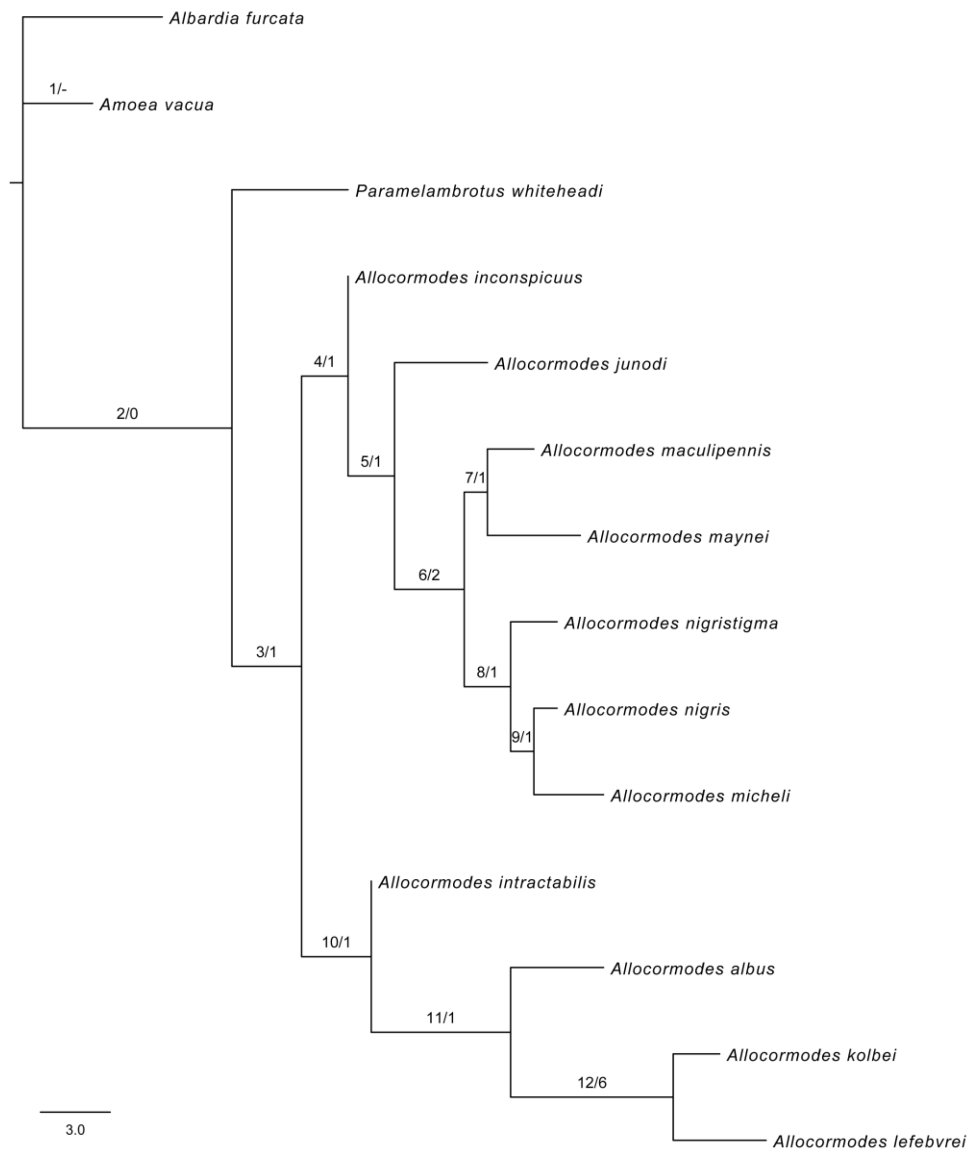
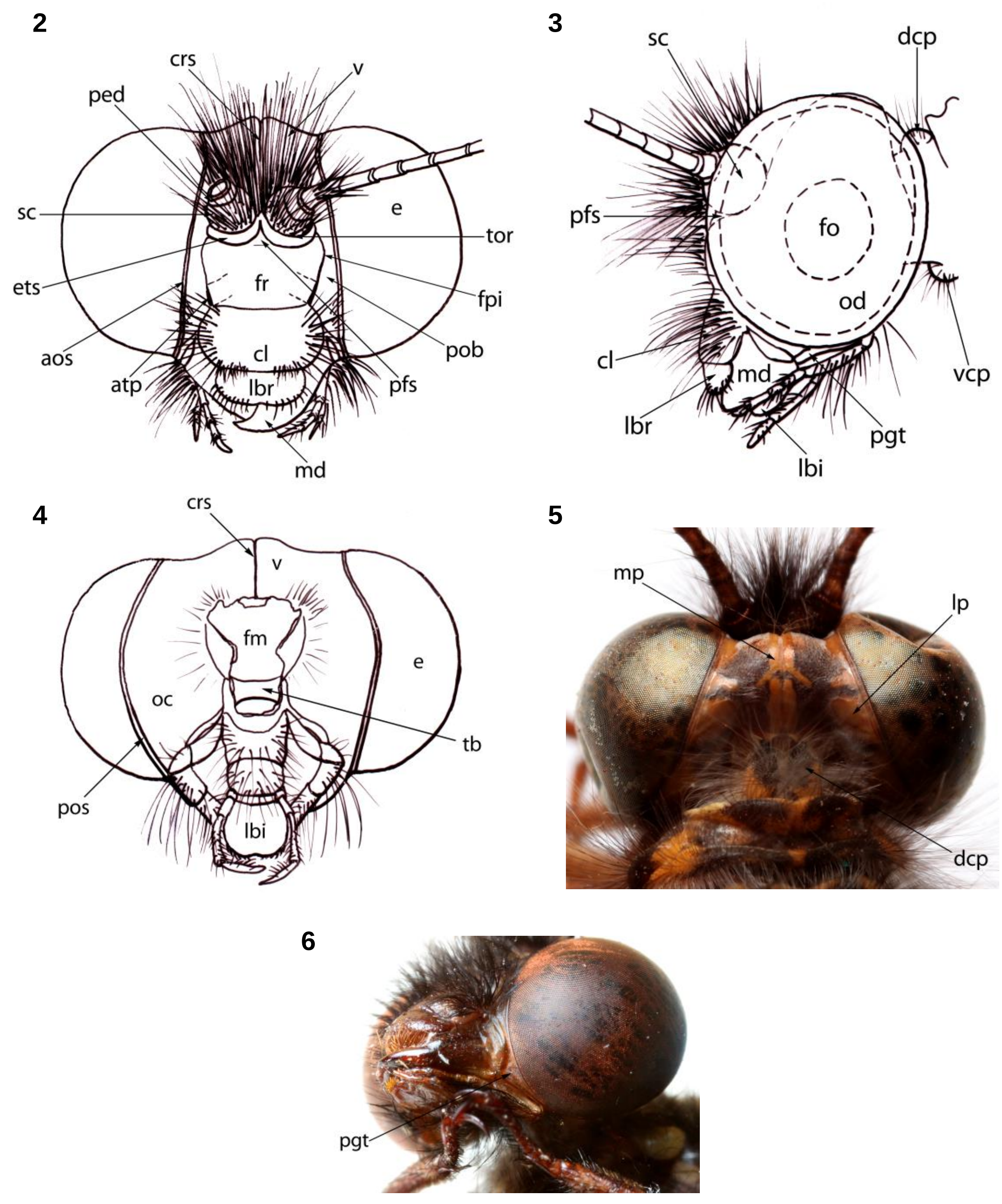
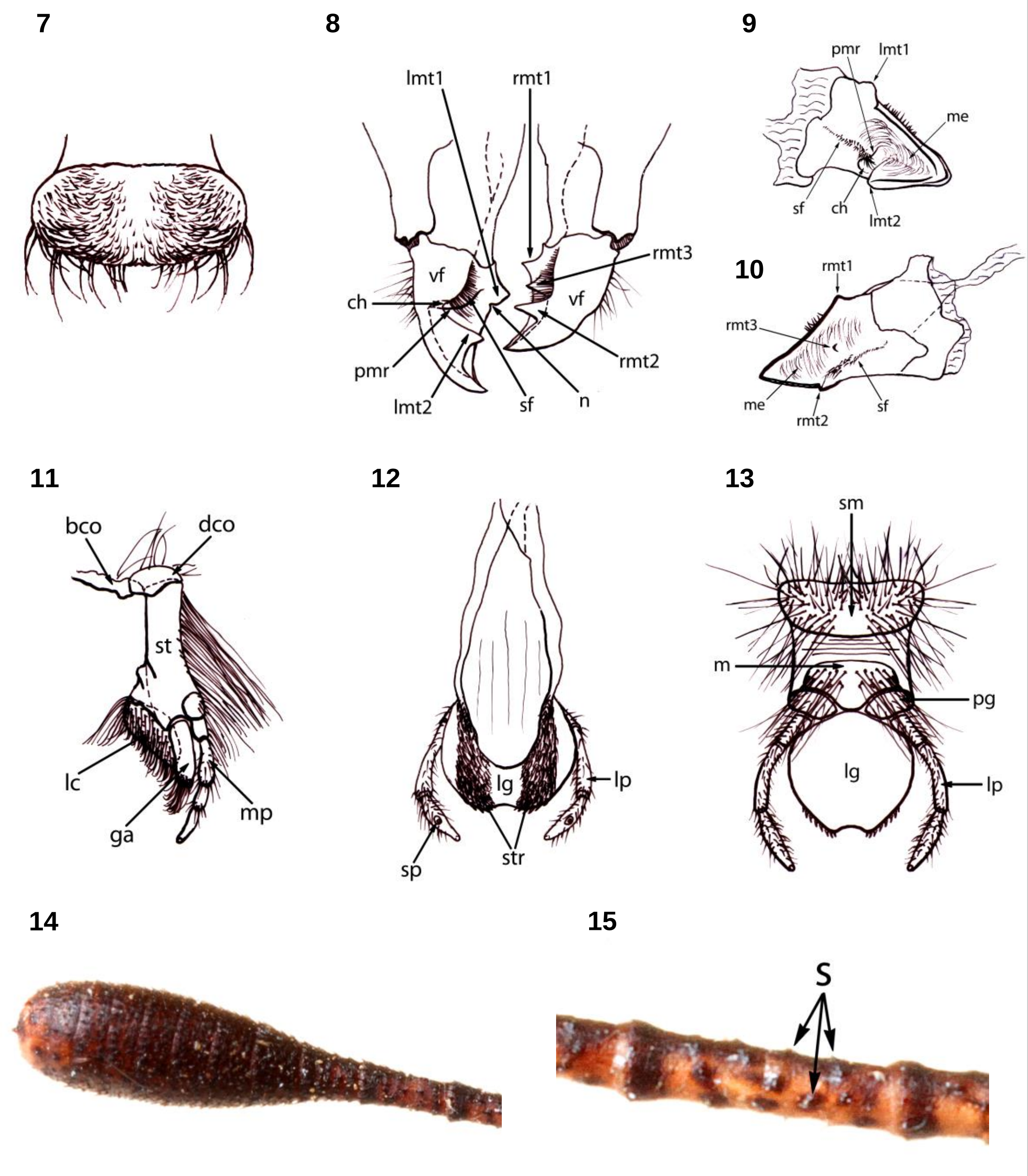


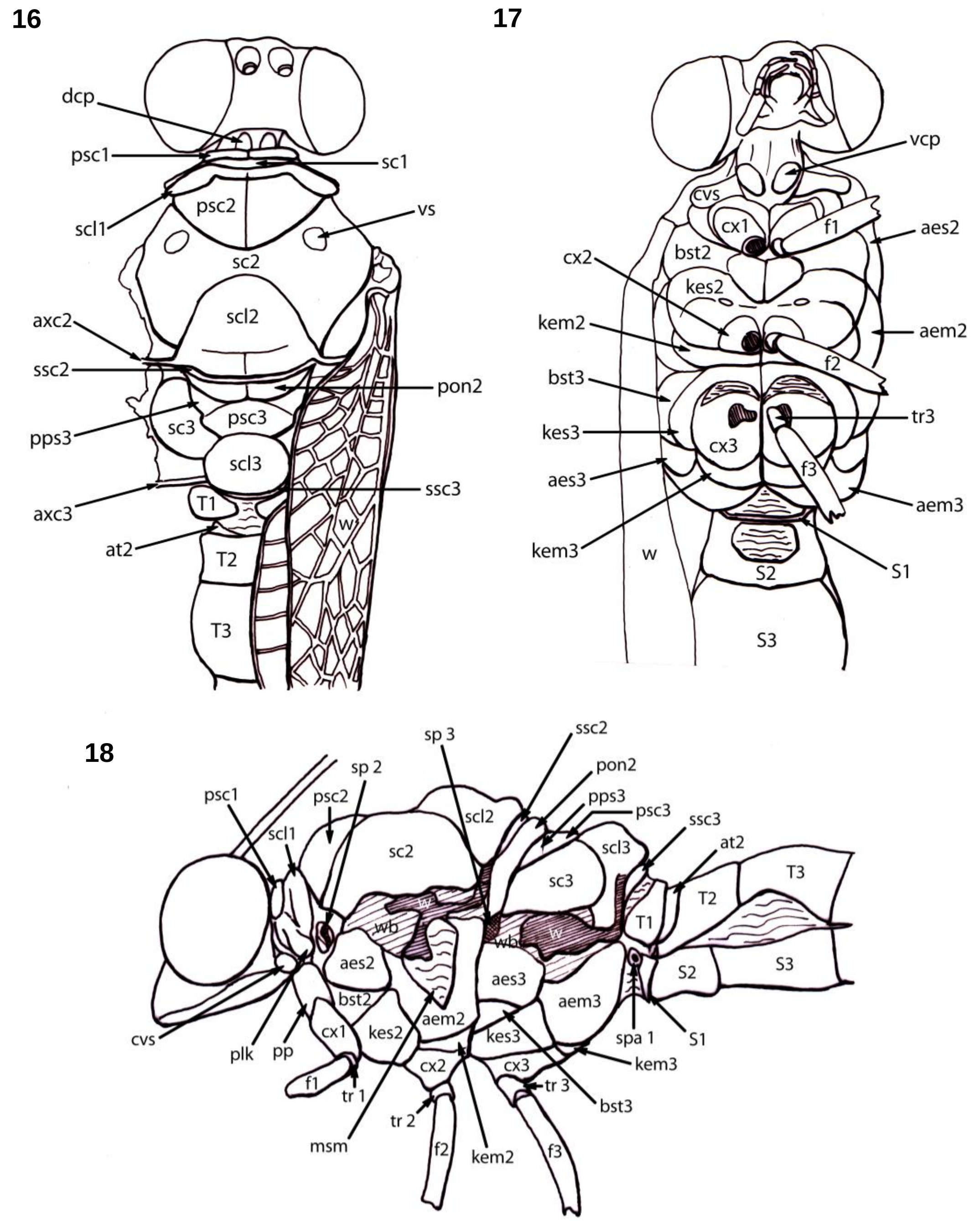
Fig. 1.—Phylogram of *Allocormodes* spp. relationships from TNT and PAUP* analysis of morphological characters, drawn to reflect branch lengths. Outgroup taxa = *Albardia furcata*, *Amoea vacua*, *Paramelambrotus whiteheadi*; # ingroup taxa = 11; # characters = 35; length = 79; C. I. = 0.7468; R. I. = 0.7015. Numbers above branches (e.g., 6/2) indicate the number of the adjacent (downstream) node followed by Bremer support value for that node. Node numbers correspond to those given in the character state change list (see A1 Table 3). For a list of node synapomorphies and terminal taxon autapomorphies see A1 Table 2 and individual taxon descriptions.



Figs. 2–6.—Head and cervix of *Allocormodes*. 2.—Head, anterior. 3.—Head and cervix (not including cervical sclerite), lateral. 4.—Head, posterior. 5.—Head, vertex. 6.—Head, ventral oblique. Abbreviations: *aos* = anterior orbital sclerite; *atp* = anterior tentorial pit; *cl* = clypeus; *crs* = coronal suture; *dcp* = dorsal cervical plate; *e* = eye; *ets* = extra-torular sclerite; *fm* = foramen magnum; *fo* = foramen orbitale; *fpi* = frons-paraocular band inflection; *fr* = frons; *lbi* = labium; *lbr* = labrum; *lp* = lateral plate; *md* = mandible; *mp* = mesal plate; *oc* = occiput; *od* = ocular diaphragm; *ped* = pedicel; *pfs* = prefrons; *pgt* = posterior genal triangle; *pob* = paraocular band; *pos* = postorbital sclerite; *sc* = scape; *tb* = tentorial bridge; *tor* = torulus; *v* = vertex; *vcp* = ventral cervical plate.



Figs. 7–15.—Mouthparts and antennae of *Allocormodes*. 7.—Labrum, ventral. 8.—Mandibles, ventral. 9.—Left mandible, mesolateral. 10.—Right mandible, mosolateral. 11.—Right maxilla, dorsal. 12.—Labium, dorsal. 13.—Labium, ventral. 14.—Antennal club. 15.—Antennal flagellomere (distal region of flagellum) with setitori. Abbreviations: *bco* = basicardo; *ch* = channel; *dco* = disticardo; *ga* = galea; *lc* = lacinia; *lg* = ligula; *lmt1* = left mandible tooth one; *lmt2* = left mandible tooth two; *lp* = labial palp; *m* = mentum; *me* = mesal excavation; *mp* = maxillary palp; n = notch; *pg* = palpiger; *pmr* = posteromesal ridge; *rmt1* = right mandibular tooth one; rmt2 = right mandibular tooth two; rmt3 = right mandibular tooth three; *s* = setitorus; *sf* = setal fringe; *sm* = submentum; *sp* = subapical pore; *st* = stipe; *str* = setal track; *vf* = ventral face.



Figs. 16–18.—Cervix, thorax, and abdominal segments 1–3 of *Allocormodes*. 16.—Dorsal. 17.—Ventral. 18.—Lateral. Abbreviations: *at* = acrotergite; *aem* = anepimeron; *aes* = anepisternum; *axc* = axillary cord; *bst* = basisternite; *cvs* = cervical sclerite; *cx* = coxa; *dcp* = dorsal cervical plate; *f* = femur; *kem* = katepimeron; *kes* = katepisternum; *msm* = mesothoracic subalar membrane; *plk* = posterolateral knob; *pon* = postnotum; *pp* = pronotal pleuron; *pps* = paraprescutum; *psc* = prescutum; *S* = sternite; *sc* = scutum; *scl* = scutellum; *sp* = spiracle; *spa 1*= abdominal spiracle 1; ; *ssc* = subscutellum; *T* = tergite; tr = trochanter; *vcp* = ventral cervical plate; *vs* = velvety spot; *w* = wing (cross section); *wb* = wing basal sclerites.

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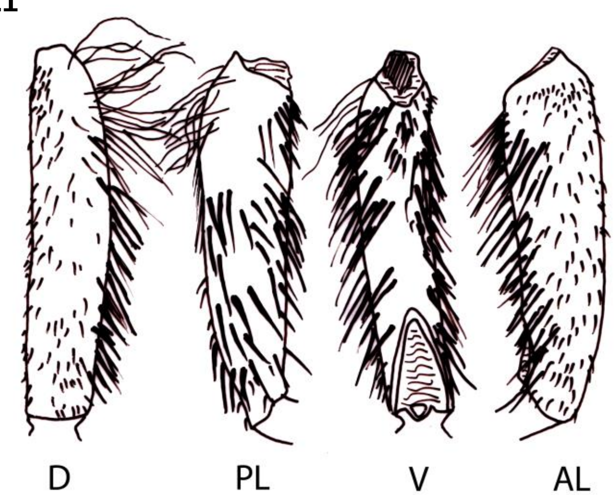

Figs. 19–21.—Leg features of *Allocormodes*. 19.—Mesothoracic leg, posterolateral, showing surfaces and integument spots, *A. micheli*. 20.—Prothoracic tibia, ventral, *A. kolbei*. 21.—Leg surfaces, mesothoracic femur, displaying various setal types and distribution patterns. Abbreviations: *AL* = anterolateral; *D* = dorsal; *PL* = posterolateral; *V* = ventral; *ac* = antennal comb.

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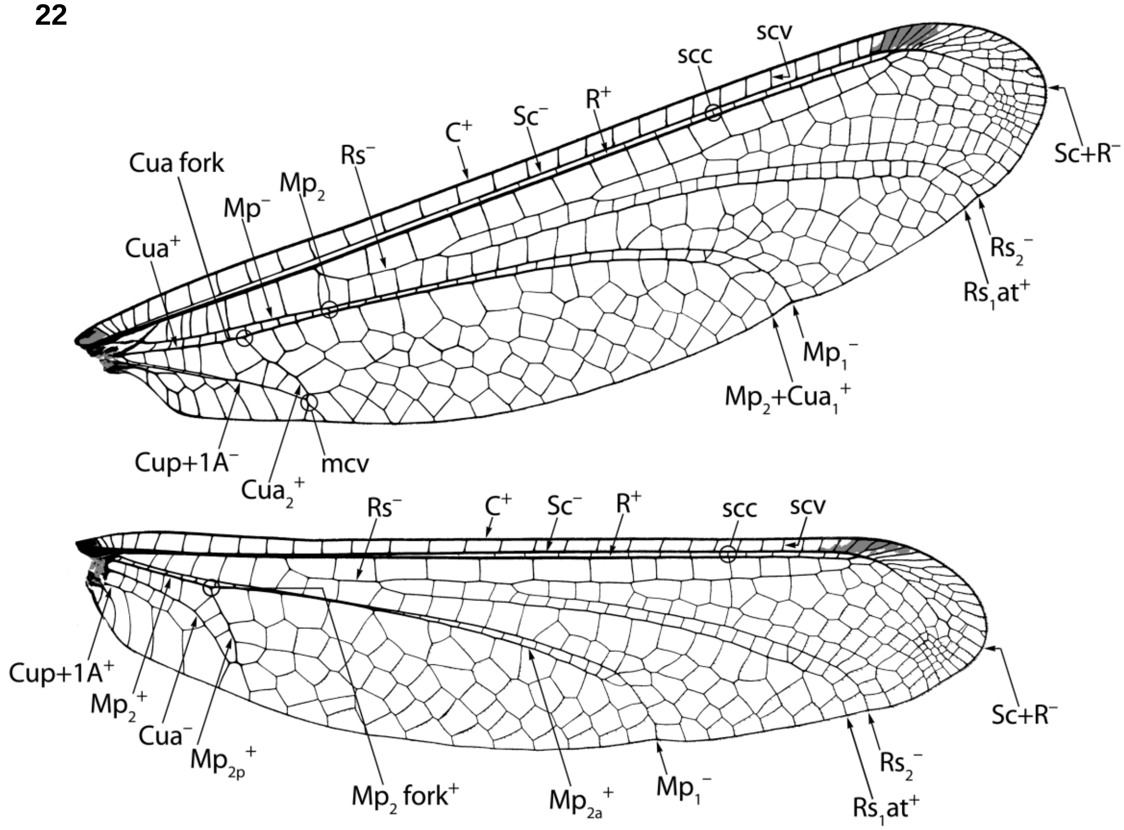

Fig. 22.—Wing venation of *Allocormodes intractabilis* ♀ (JRJ_00019), showing convex (+) and concave (–) veins. Abbreviations: *1A* = first anal vein; *C* = costa; *Cua* = cubitus anterior; *Cup* = cubitus posterior; *mcv* = marginal crossvein; *Mp* = media posterior; *R* = radius; *Rs* = radial sector ; Rs_1at = radial sector one anterior trace; *Sc* = subcosta; *scc* = subcostal crossvein; *scv* = subcostal veinlet.

23

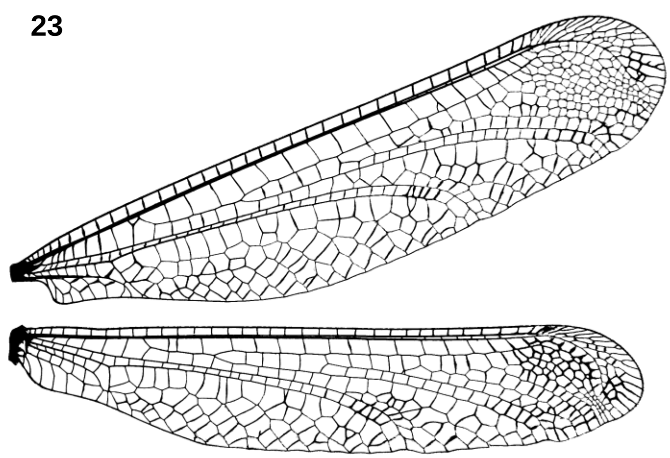

Fig. 23.—Wing venation of *Allocormodes lefebvrei* ♂ (JRJ_00035).

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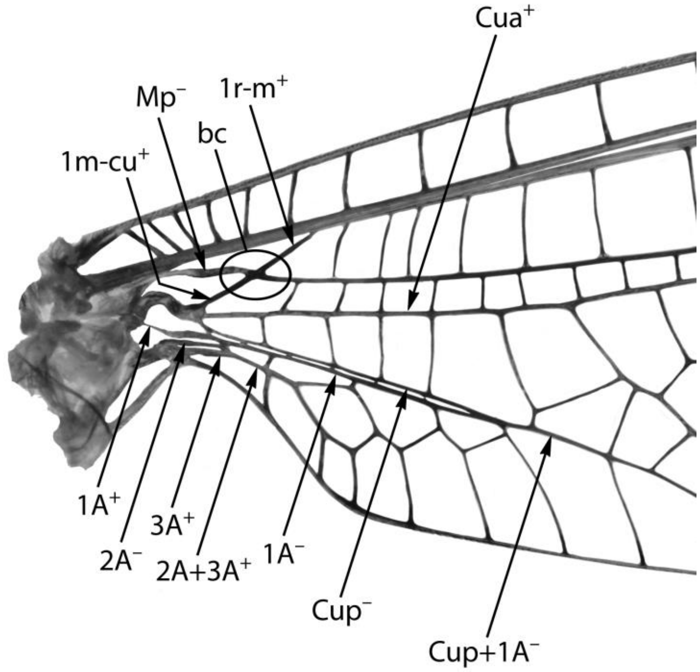

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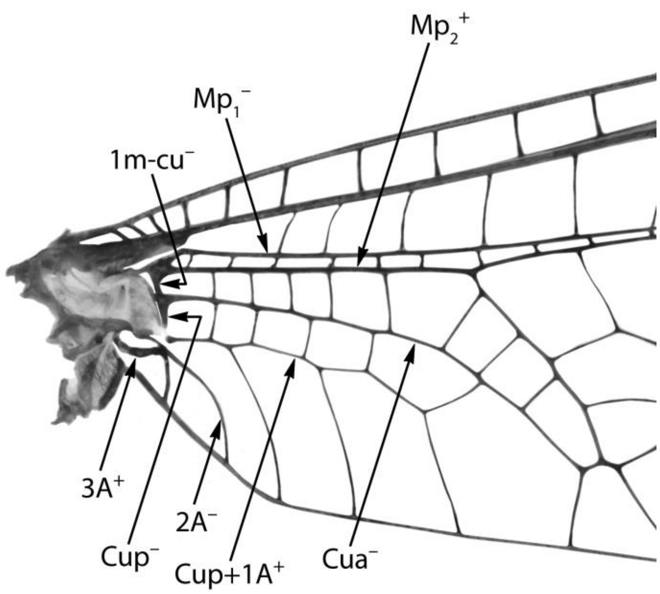


Figs. 24–25.—Basal wing venation of *Allocormodes intractabilis* ♀ (JRJ_00019). 24.—Forewing. 25.—Hind wing. Abbreviations: *#A* = anal veins; *bc* = basal chiasma; *Cua* = cubitus anterior; *1m-cu* = first medio-cubital crossvein; *Cup* = cubitus posterior; *Mp* = media posterior; *1r-m* = first radio-medial crossvein.

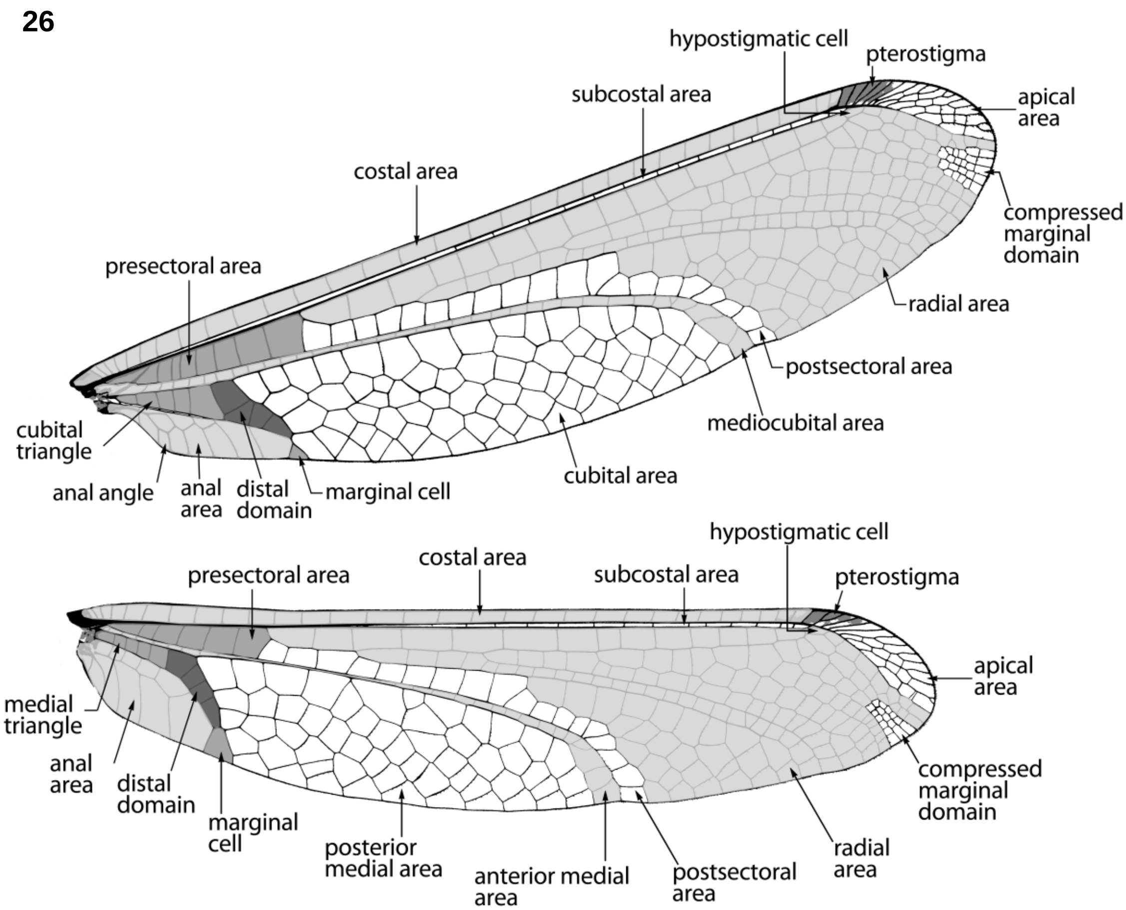
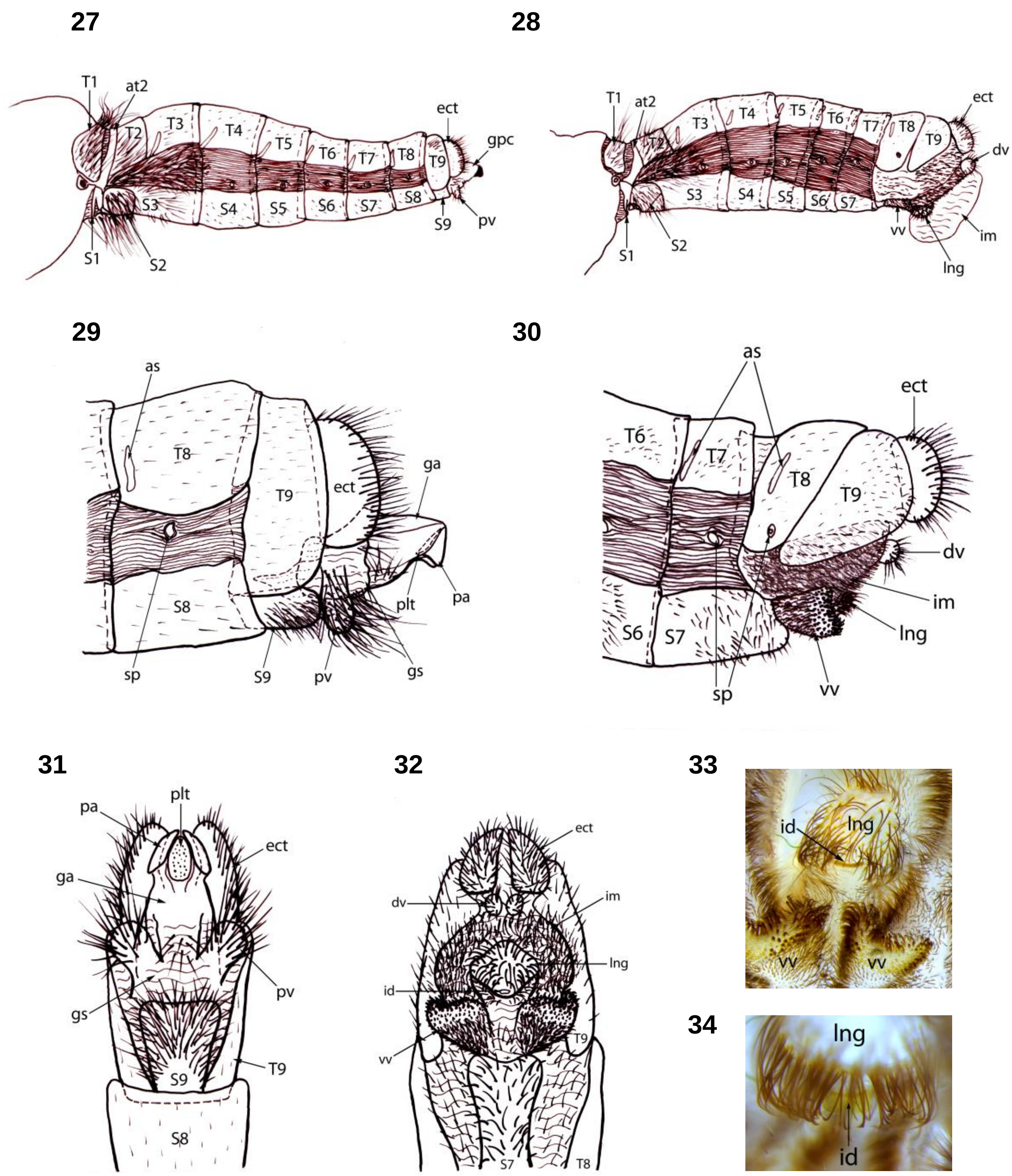


Fig. 26.—Wing areas of *Allocormodes intractabilis* ♀ (JRJ_00019). The compressed marginal domain is a sub-element of the radial area; the distal domains are the distal portions of the cubital and medial triangles, respectively.



Figs. 27–34.—Abdomens and terminalia of *Allocormodes*. 27.—Abdomen, male, lateral, GPC fully everted. 28.—Abdomen, female, lateral, right internal membrane completely everted. 29.—Apex of abdomen, male, lateral, GPC fully everted. 30.—Apex of abdomen, female, lateral. 31.—Apex of abdomen, male, ventral, GPC fully everted. 32.—Apex of abdomen, female, ventral, linguella fully everted. 33.—Linguella and interdens, posterior view, *A. junodi*. 34.—Interdens, dorsal view, *A. junodi*. Abbreviations: ***as*** = antecostal scar; ***at*** = acrotergite; ***dv*** = distivalve; ***ect*** = ectoproct; ***ga*** = gonarcus; ***gs*** = gonosaccus; ***id*** = interdens; ***im*** = internal membrane; ln***g*** = linguella; ***plt*** = pelta; ***pa*** = paramere; ***pv*** = pulvinus; ***S#*** = sternites; ***sp*** = spiracle; ***T#*** = tergites; ***vv*** = ventrovalve.

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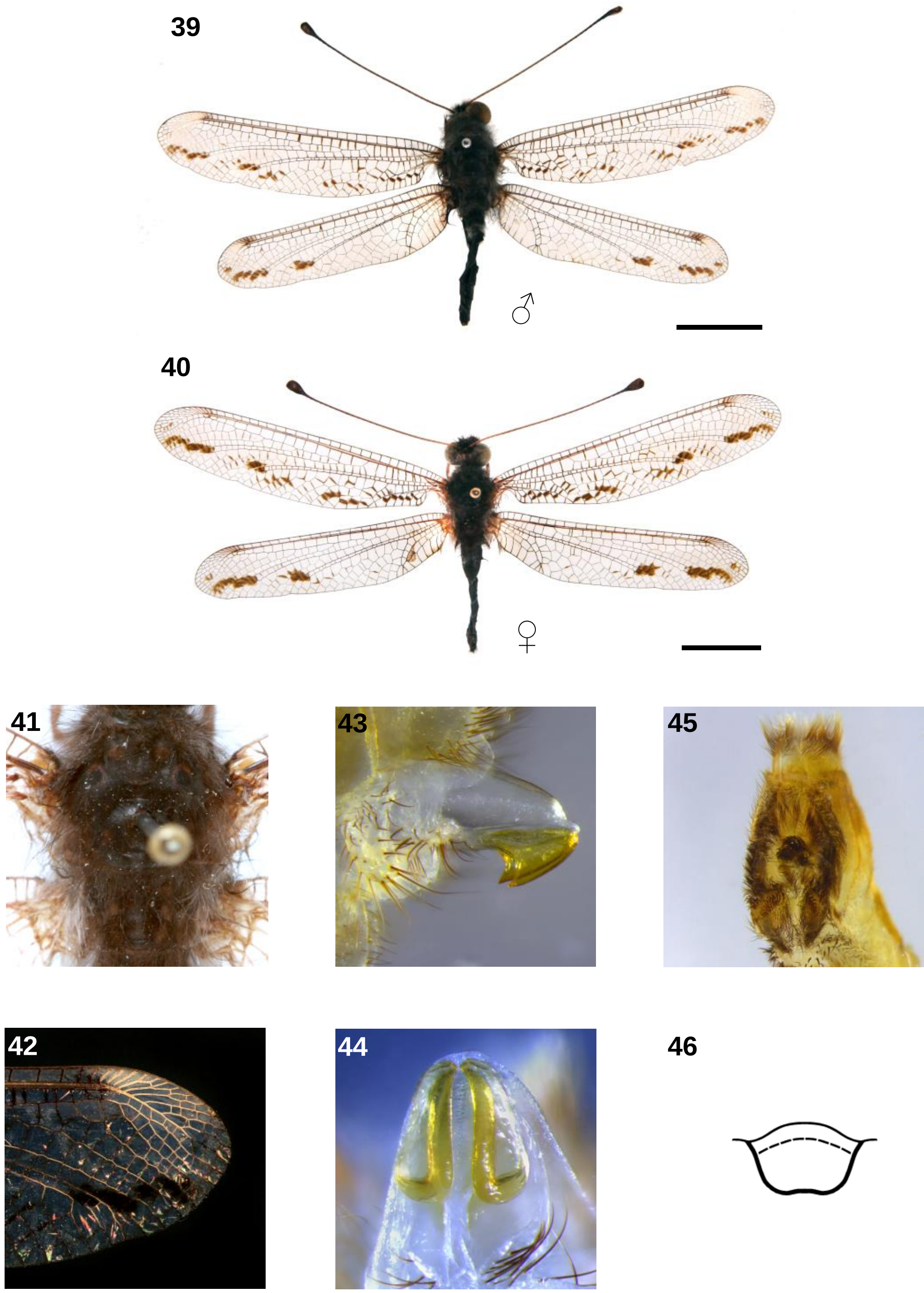
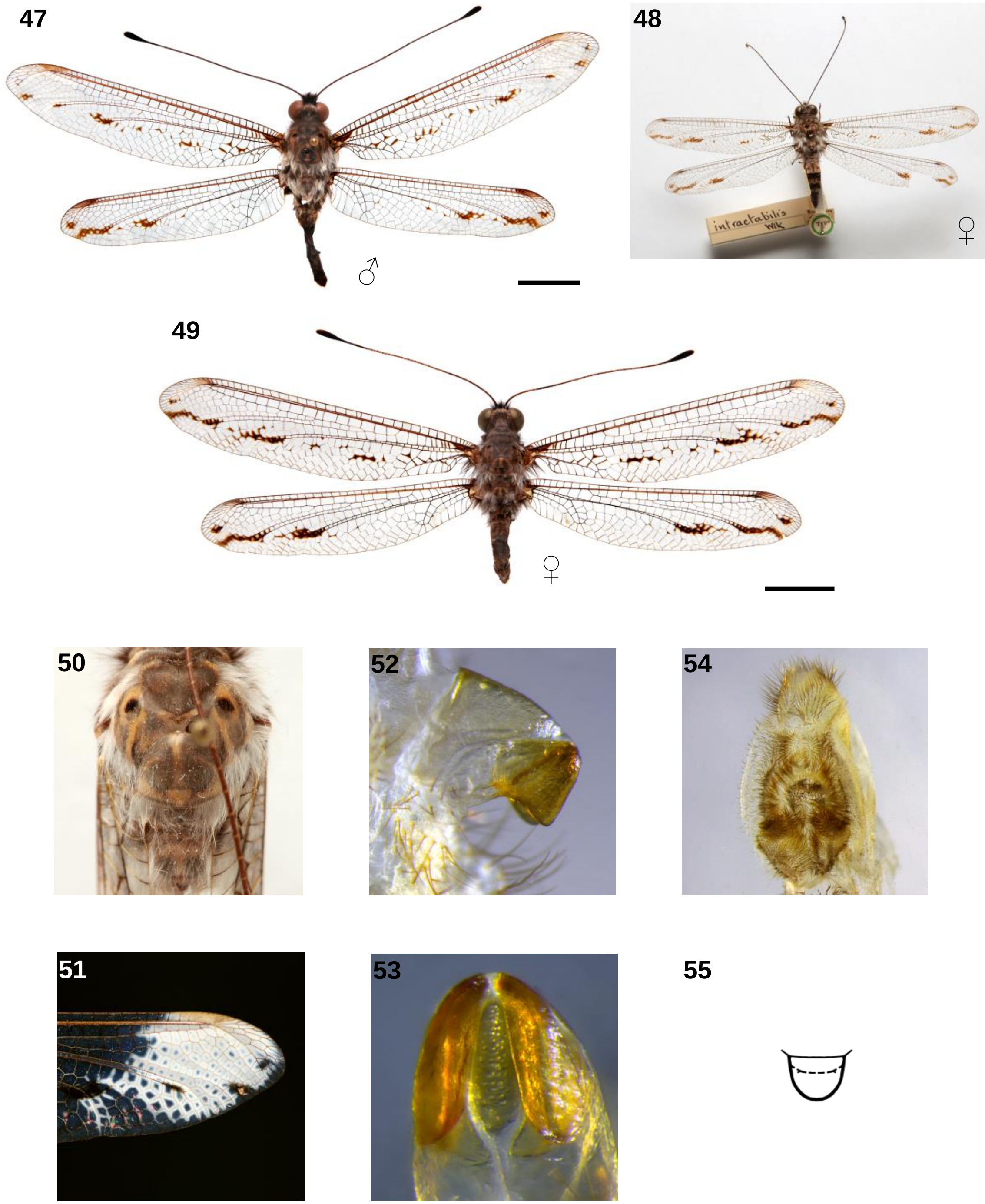
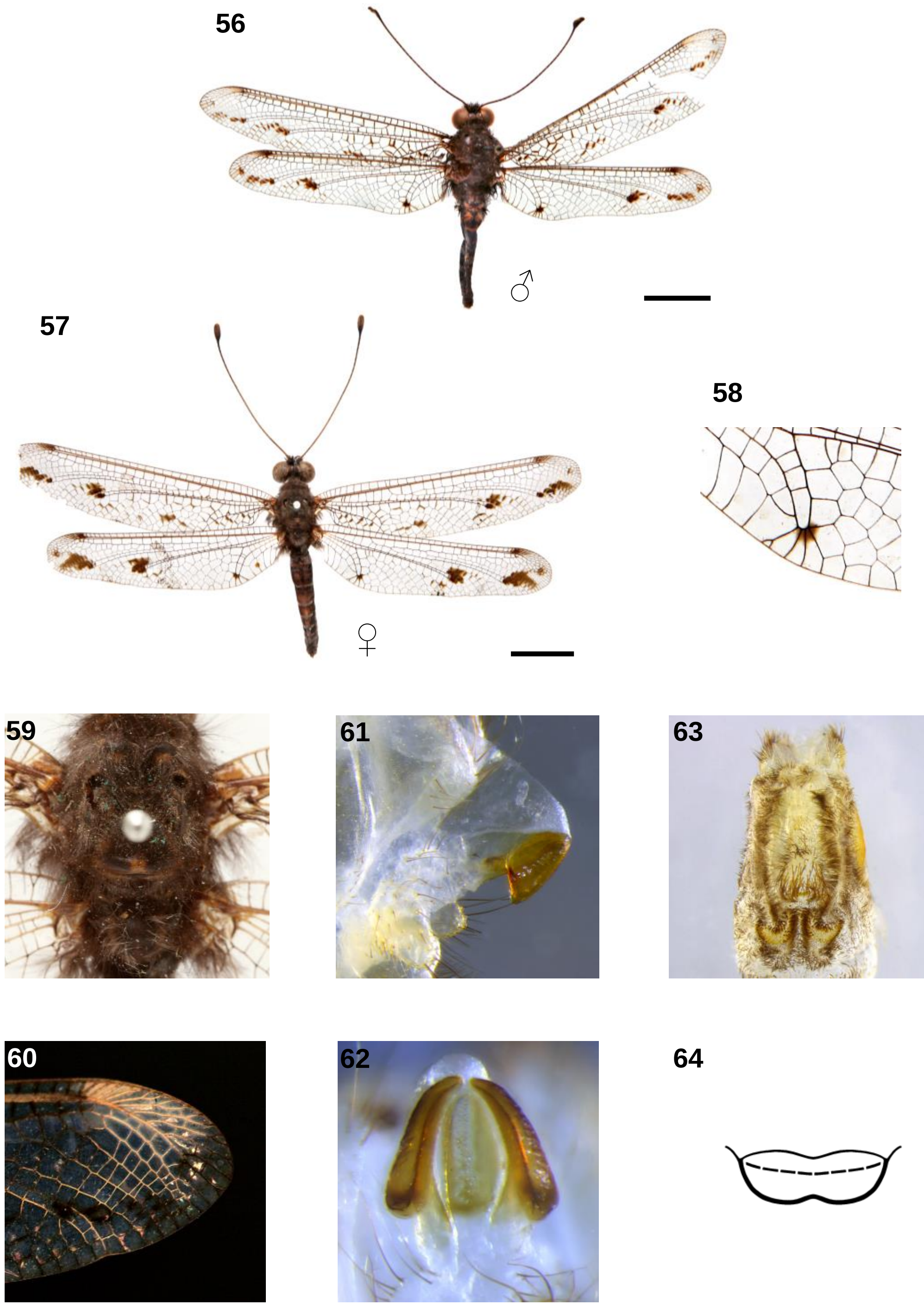
Figs. 35–38.—*Allocormodes albus* n. sp., holotype ♀, BMNH, JRJ_01205. 035.—Habitus, dorsal. 36.—Pterothorax, dorsal. 37.—Apex of abdomen, posterior; specimen is in poor condition, with ventral portions torn apart. 38.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



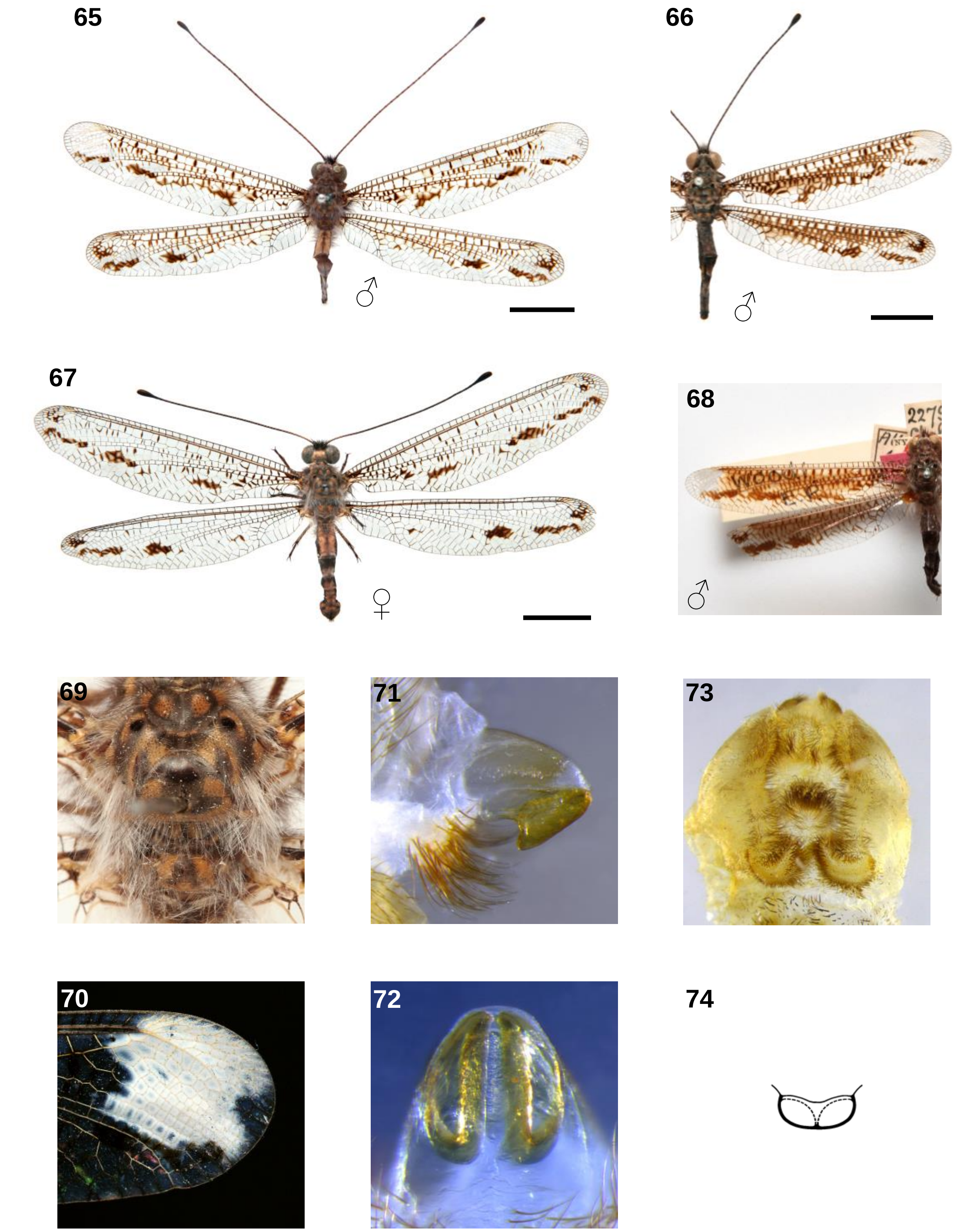
Figs. 39–46.—*Allocormodes inconspicuus* n. sp. 39.—Habitus, dorsal, paratype ♂, JRJ_001191. 40.—Habitus, dorsal, holotype ♀, CAS, JRJ_00020. 41.—Pterothorax, dorsal. 42.—Apex of forewing, ♂. 43.—GPC and pulvini, lateral. 44.—GPC and pelta, ventral. 45.—Apex of abdomen, ♀, posterior. 46.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



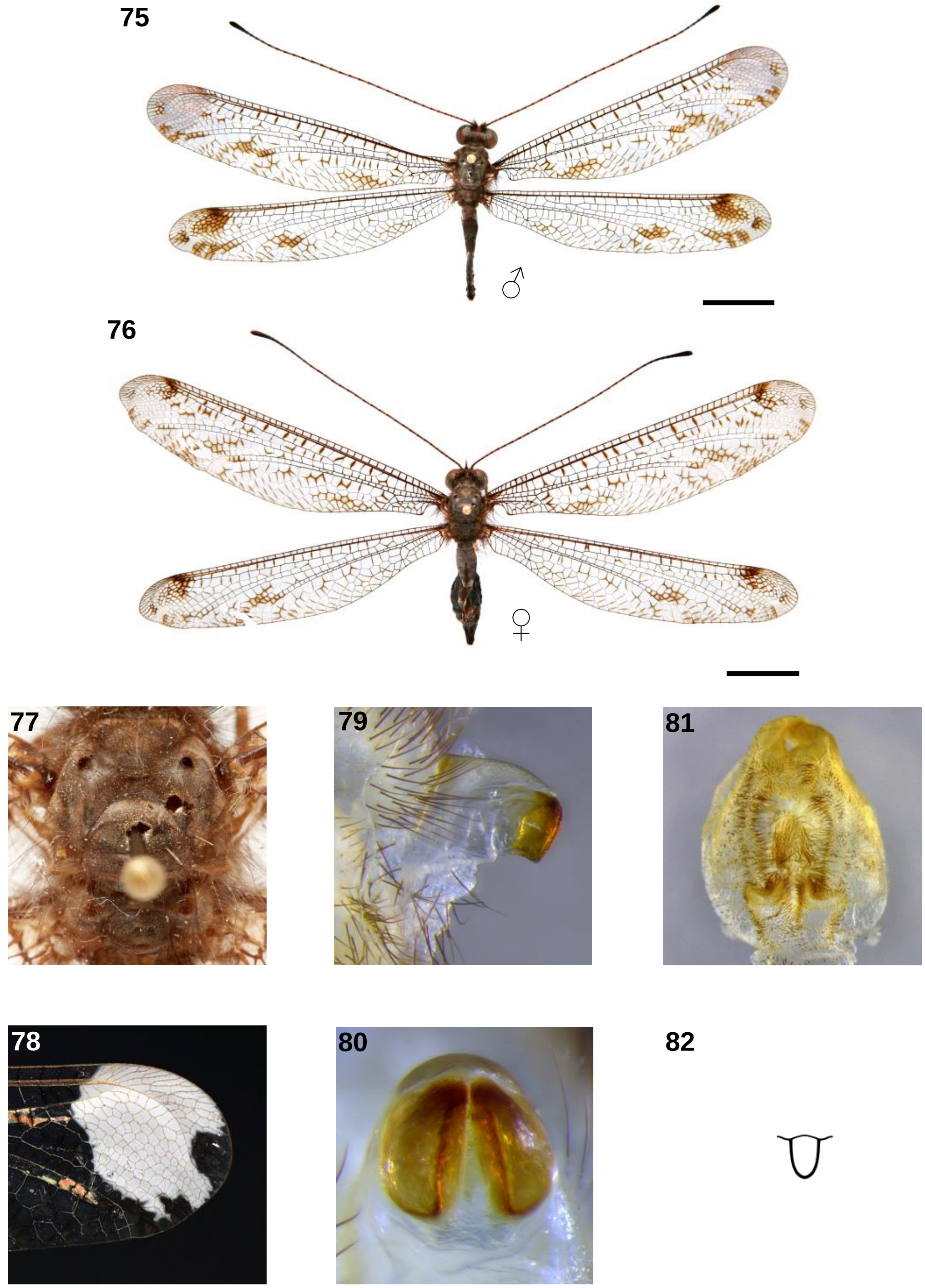
Figs. 47–55.—*Allocormodes intractabilis*. 47.—Habitus, dorsal, non-type ♂, JRJ_00003. 48.—Habitus, dorsal, holotype ♀, BMNH, no JRJ label applied. 49.—Habitus, dorsal, non-type ♀, JRJ_00014. 50.—Pterothorax, dorsal. 51.—Apex of forewing, ♂. 52.—GPC and pulvini, lateral. 53.—GPC and pelta, ventral. 54.—Apex of abdomen, ♀, posterior. 55.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



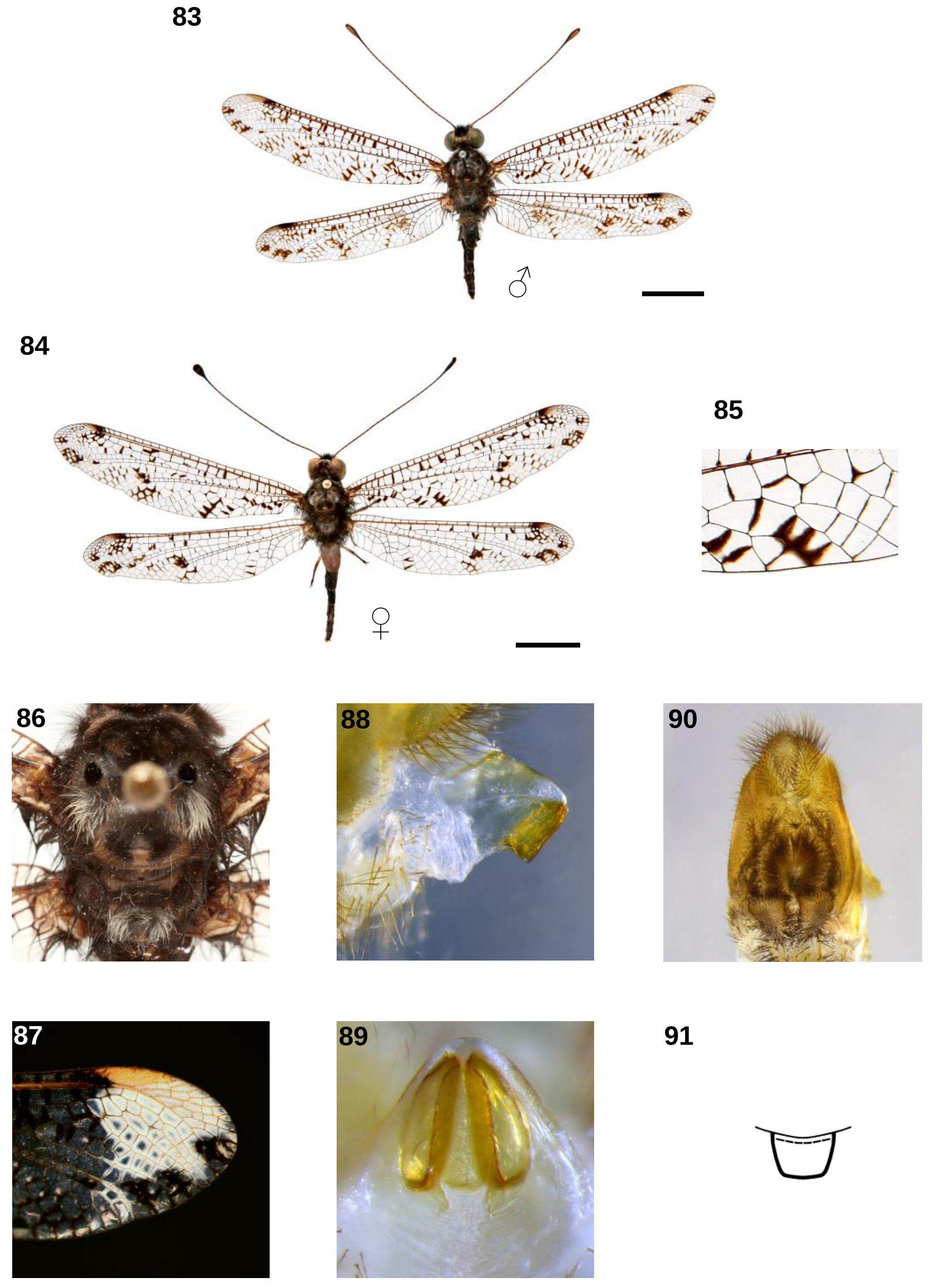
Figs. 56–64.—*Allocormodes junodi*. 56.—Habitus, dorsal, lectoype ♂, MNHN, JRJ_01214. 57.—Habitus, dorsal, non-type ♀, JRJ_01211. 58.—Posterior base of hind wing. 59.—Pterothorax, dorsal. 60.—Apex of forewing, ♂. 61.—GPC and pulvini, lateral. 62.—GPC and pelta, ventral. 63.—Apex of abdomen, ♀, posterior. 64.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



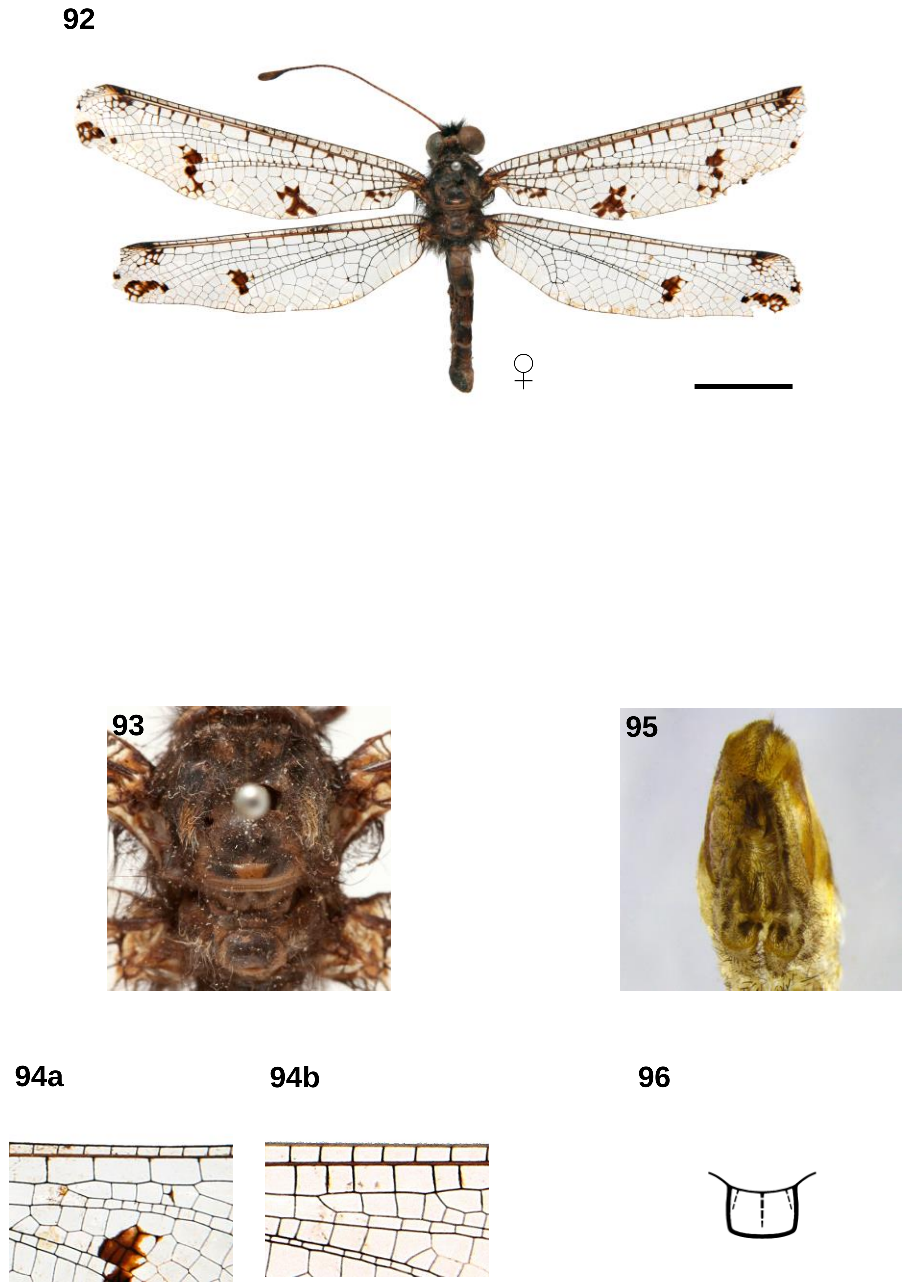
Figs. 65–74.—*Allocormodes kolbei*. 65.—Habitus, dorsal, non-type ♂, JRJ_00030. 66.—Habitus, dorsal, melanistic non-type ♂, JRJ_00049. 67.—Habitus, dorsal, non-type ♀, JRJ_01187. 68.—Habitus, dorsal, holotype ♂ of *A. woodi*, BMNH, no JRJ label applied. 69.—Pterothorax, dorsal. 70.—Apex of forewing, ♂. 71.—GPC and pulvini, lateral. 72.—GPC and pelta, ventral. 73.—Apex of abdomen, ♀, posterior. 74.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



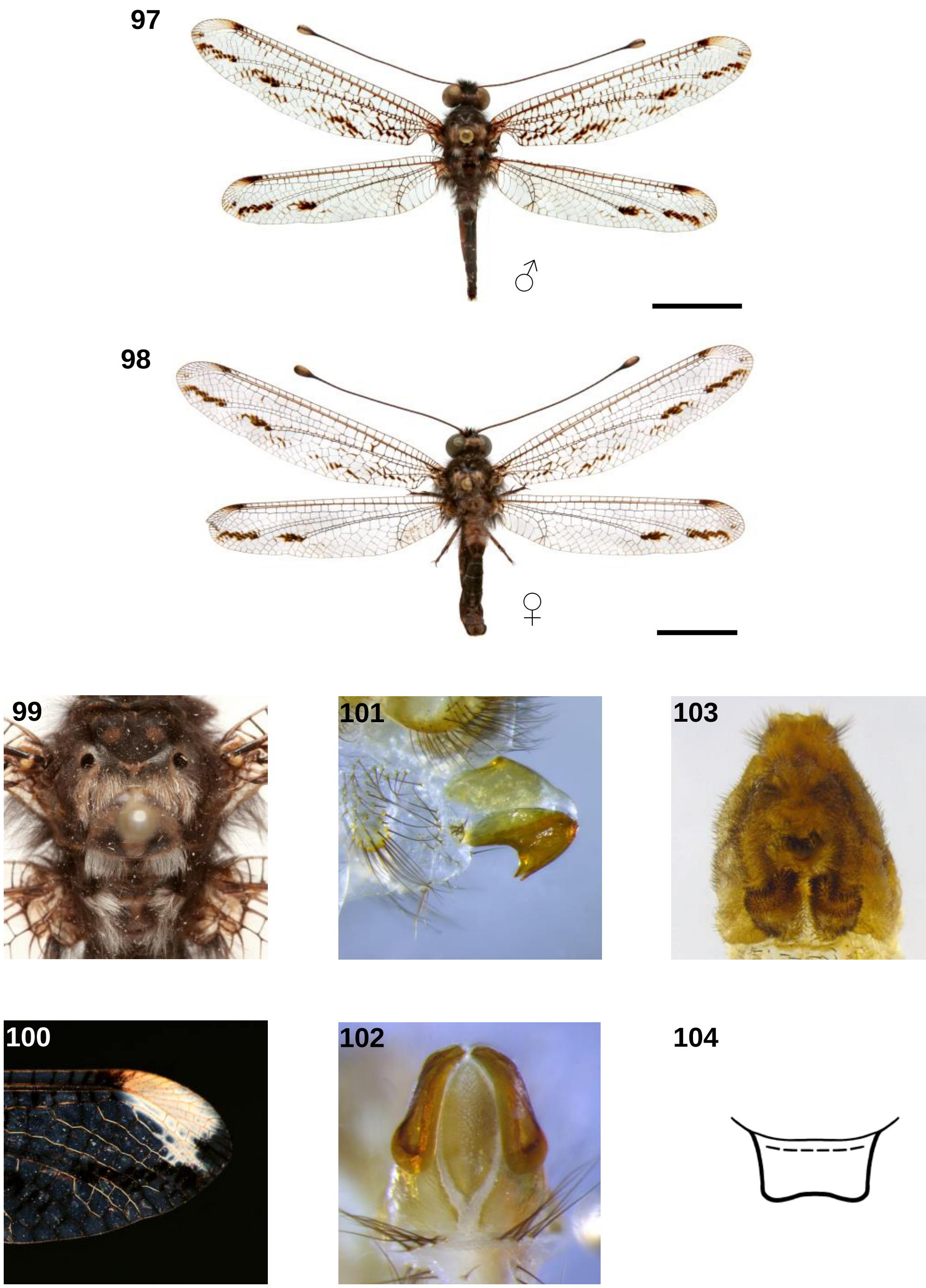
Figs. 75–82.—*Allocormodes lefebvrei*. 75.—Habitus, dorsal, non-type ♂, JRJ_00035. 76.—Habitus, dorsal, non-type ♀, JRJ_00037. 77.—Pterothorax, dorsal. 78.—Apex of forewing, ♂, JRJ_00035. 79.—GPC and pulvini, lateral. 80.—GPC and pelta, ventral. 81.—Apex of abdomen, ♀, posterior. 82.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



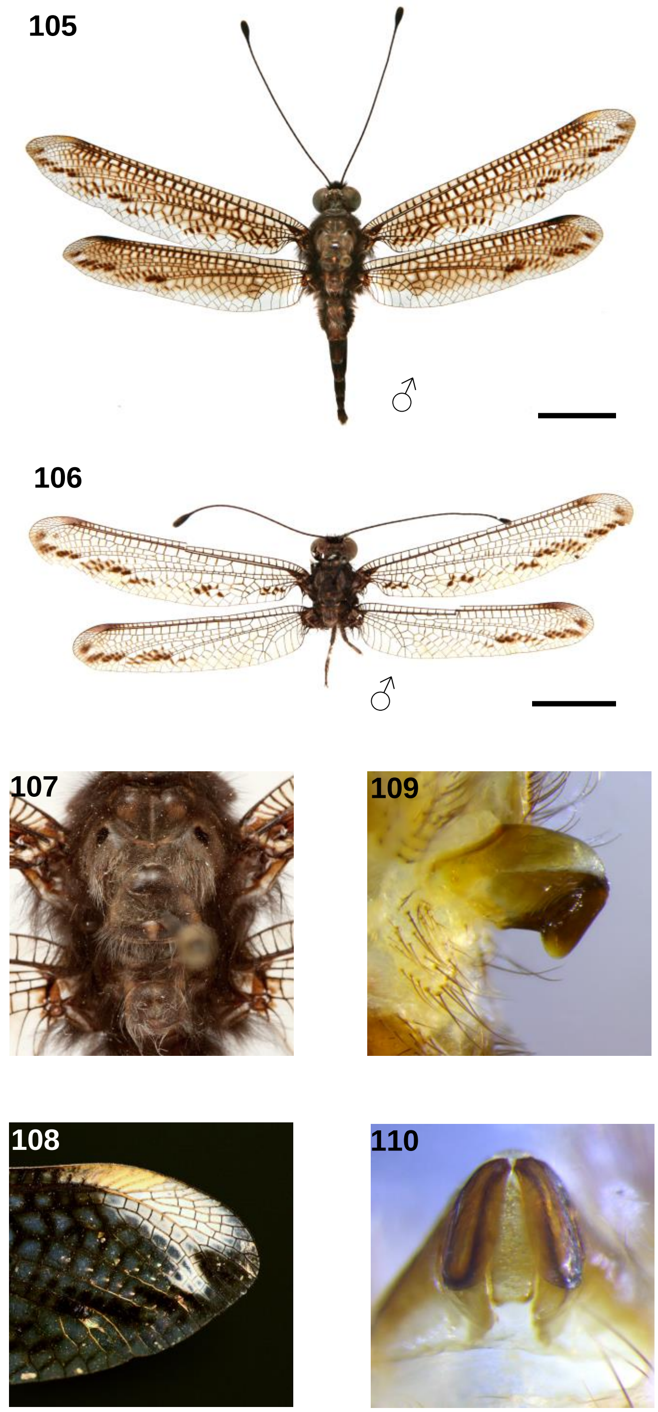
Figs. 83–91.—*Allocormodes maculipennis*. 83.—Habitus, dorsal, non-type ♂, JRJ_00039. 84.—Habitus, dorsal, non-type ♀, JRJ_00043. 85.—Posterior base of forewing. 86.—Pterothorax, dorsal. 87.—Apex of forewing, ♂. 88—GPC and pulvini, lateral. 89.—GPC and pelta, ventral. 90.—Apex of abdomen, ♀, posterior. 91.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



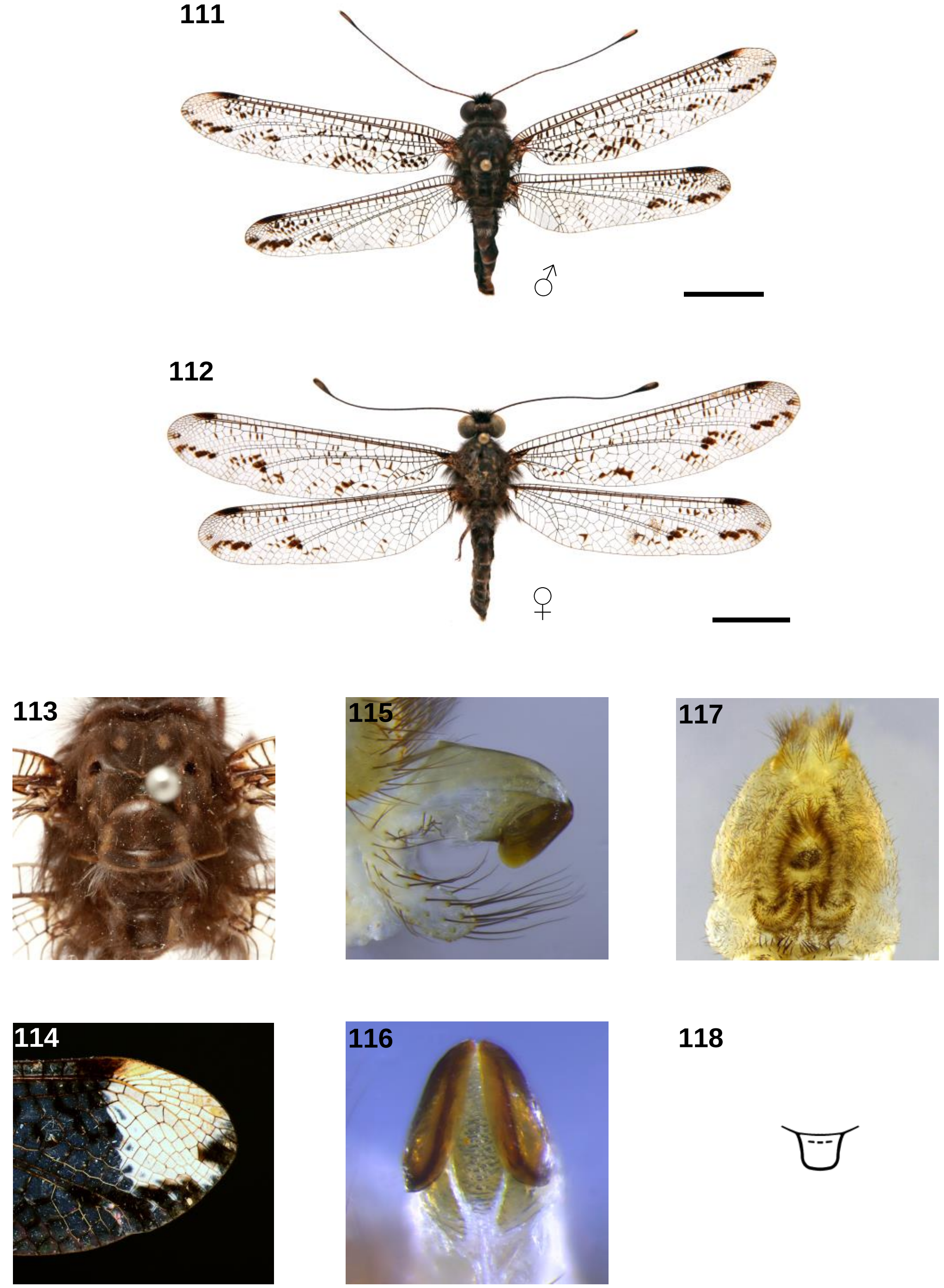
Figs. 92–96.—*Allocormodes maynei*. 92.—Habitus, dorsal, lectotype ♀, RMCA, JRJ_01190. 93.—Pterothorax, dorsal. 94a.—Right forewing, anteromesal area; note enlarged cells subtending R. 94b.—Right forewing, anteromesal area, *A. inconspicuus*; note non-enlarged cells. 95.—Apex of abdomen, ♀, posterior. 96.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



Figs. 97–104.—*Allocormodes micheli* n. sp. 97.—Habitus, dorsal, holotype ♂, USNM, JRJ_00021. 98.—Habitus, dorsal, paratype ♀, JRJ_00025. 99.—Pterothorax, dorsal. 100.—Apex of forewing, ♂. 101.—GPC and pulvini, lateral. 102.—GPC and pelta, ventral. 103.—Apex of abdomen, ♀, posterior. 104.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.



Figs. 105–110.—*Allocormodes nigris* n. sp. 105.—Habitus, dorsal, holotype ♂, MNHN, JRJ_01212. 106.—Habitus, dorsal, paratype ♂, non-melanistic, JRJ_00028 (abdomen removed). 107.—Pterothorax, dorsal. 108.—Apex of forewing, ♂. 109.—GPC and pulvini, lateral. 110.—GPC and pelta, ventral. Scale bar = 10 mm.



Figs. 111–118.—*Allocormodes nigristigma* n. sp. 111.—Habitus, dorsal, holotype ♂, UMSP, JRJ_00029. 112.—Habitus, dorsal, paratype ♀, JRJ_00047. 113.—Pterothorax, dorsal. 114.—Apex of forewing, ♂. 115.—GPC and pulvini, lateral. 116.—GPC and pelta, ventral. 117.—Apex of abdomen, ♀, posterior. 118.—Interdens, dorsal (macerated specimen). Scale bar = 10 mm.

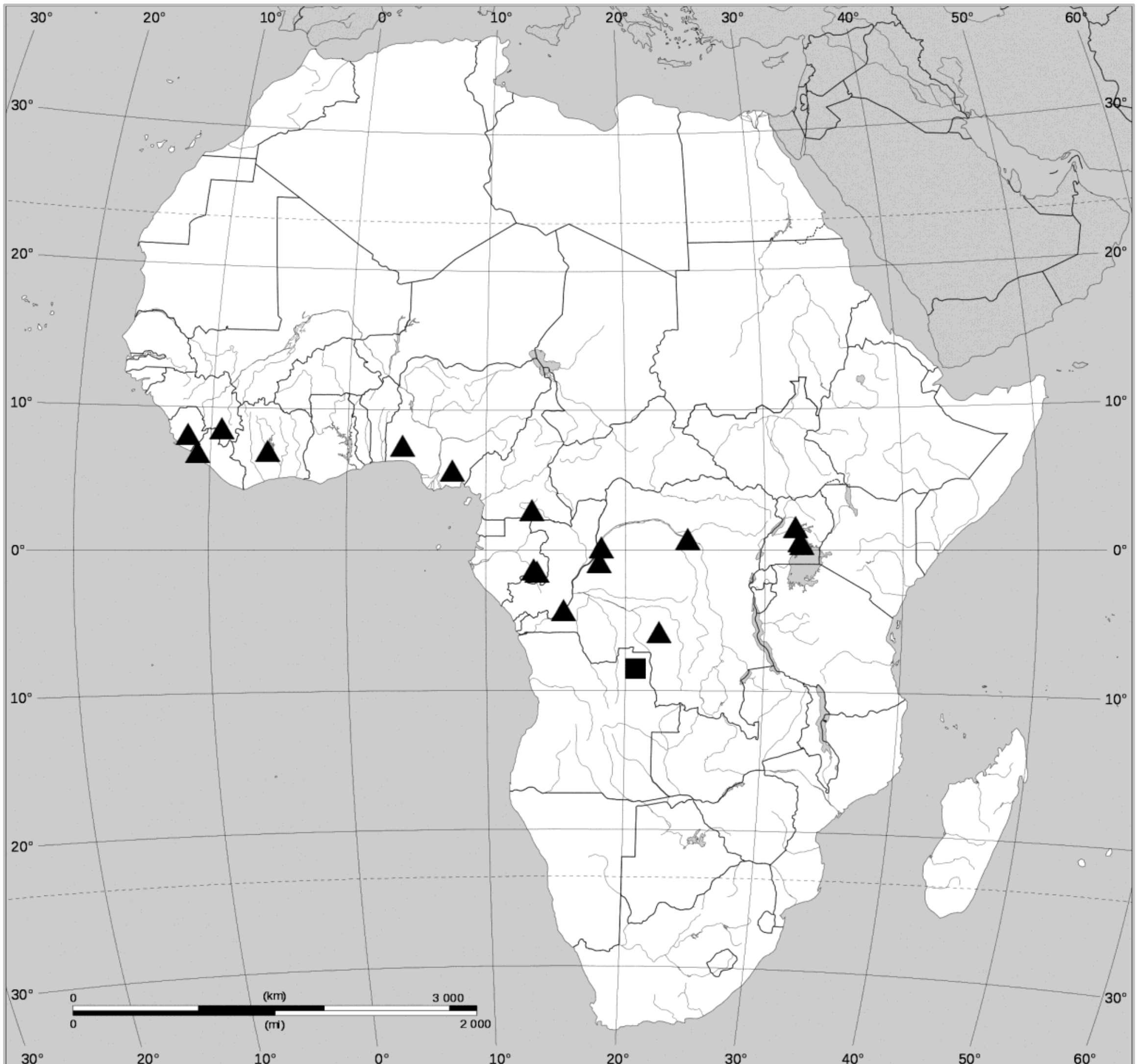


Fig. 119.—Distribution map of *Allocormodes*: *A. albus* [■]; *A. nigristigma* [▲].

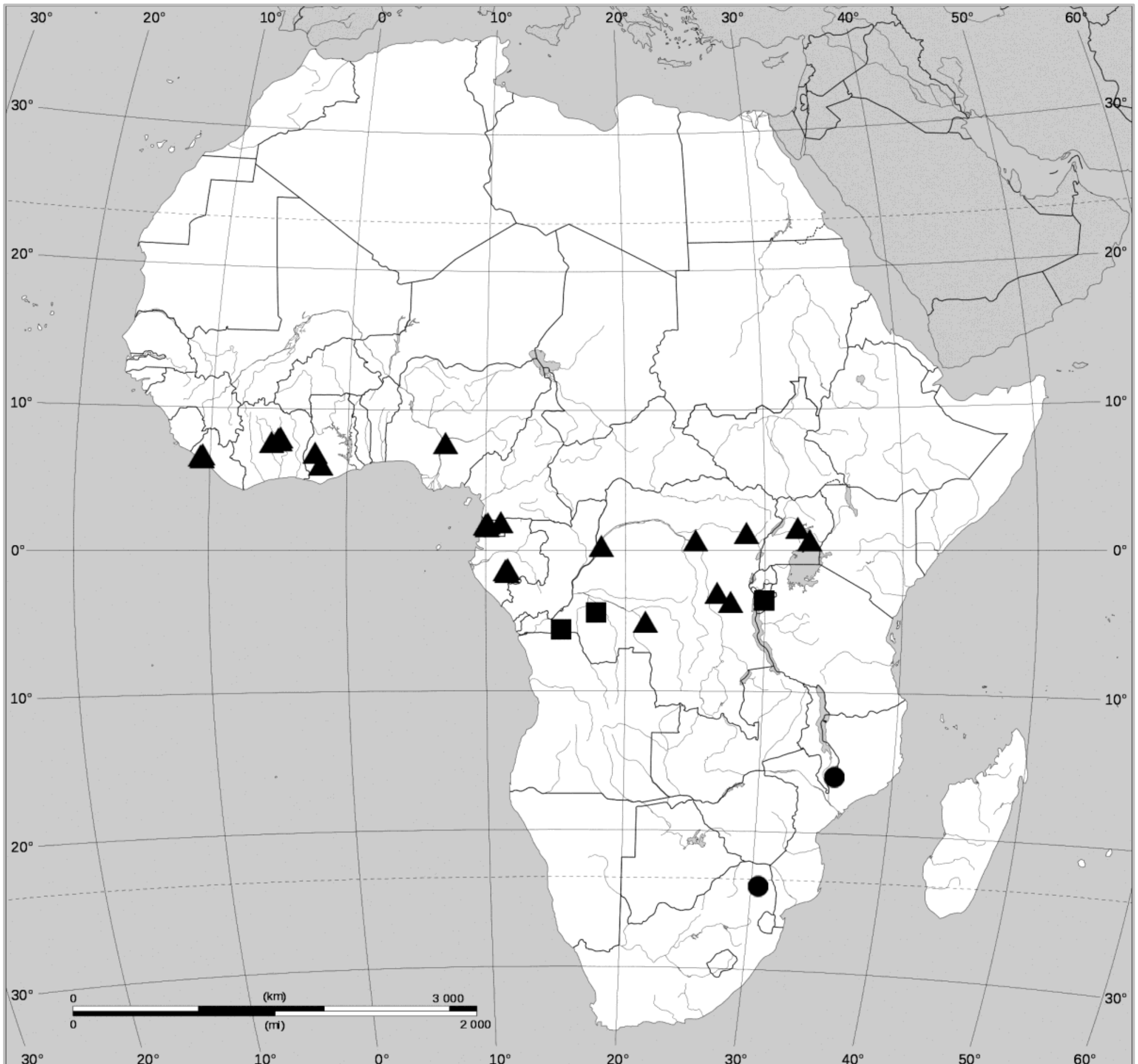


Fig. 120.—Distribution map of *Allocormodes*: *A. inconspicuus* [■]; *A. intractabilis* [▲]; *A. junodi* [●].

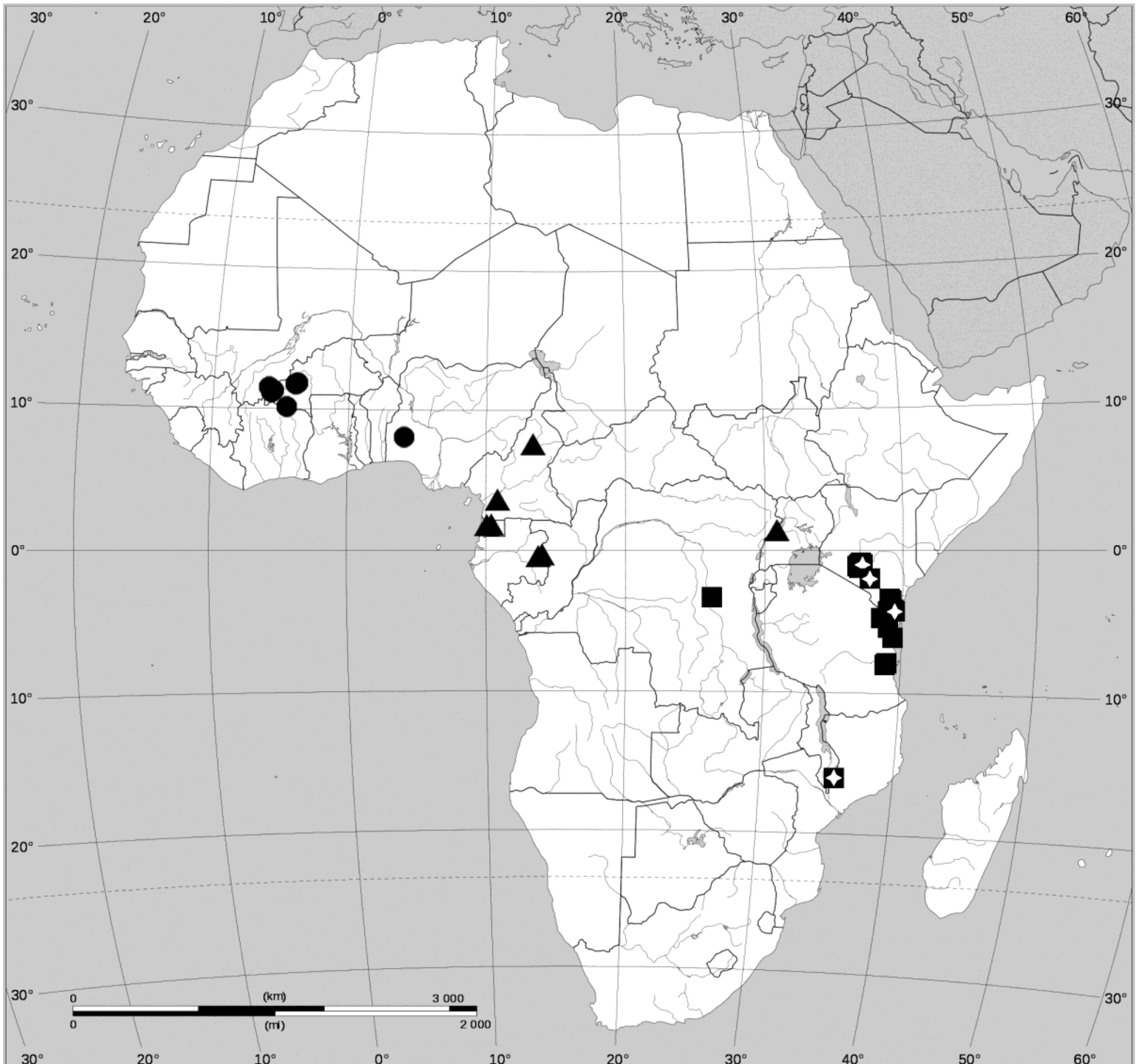


Fig. 121.—Distribution map of *Allocormodes*: *A. kolbei* [■]; *A. kolbei* melanistic males [■ with white star]; *A. lefebvrei* [▲]; *A. micheli* [●].

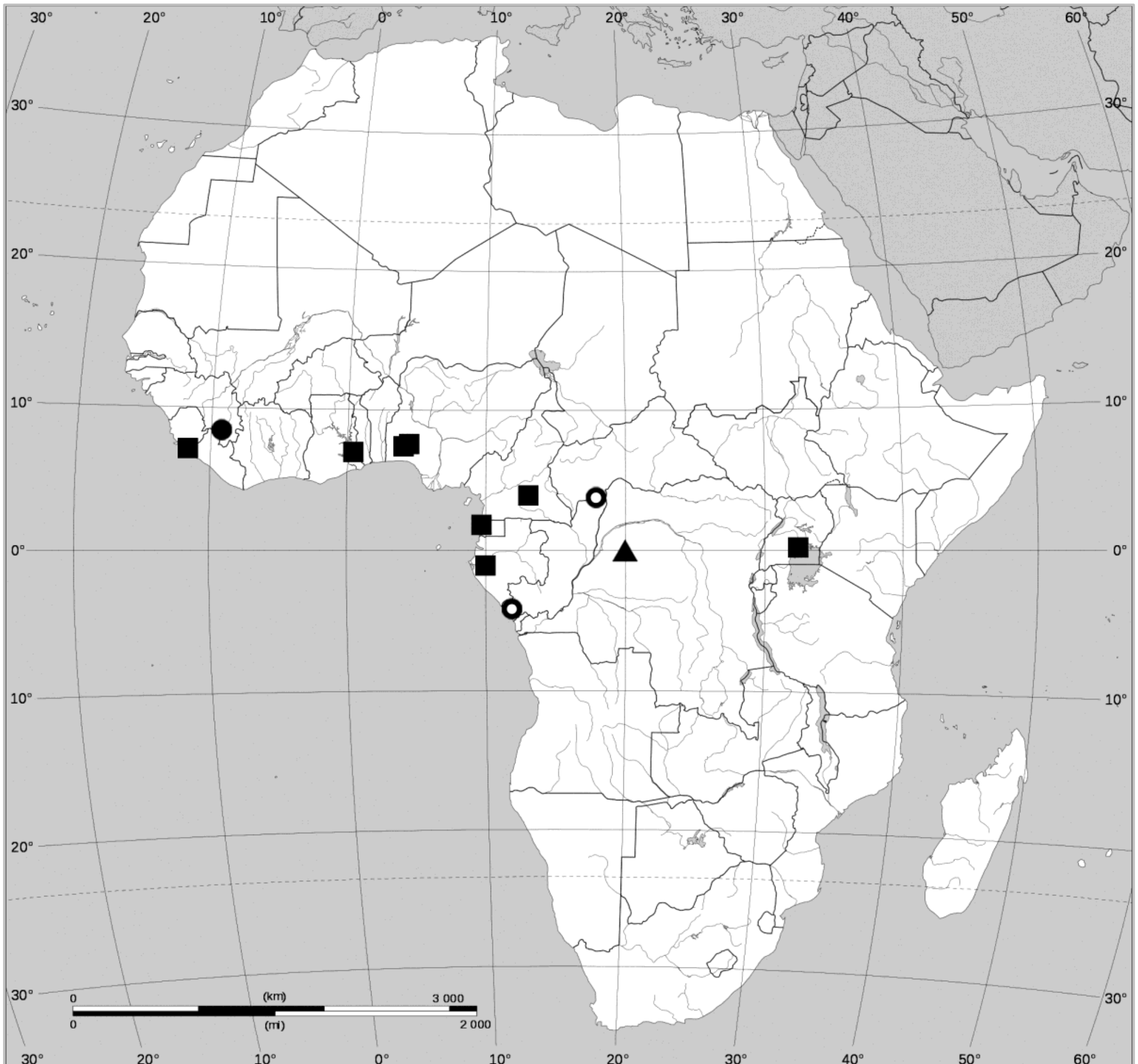


Fig. 122.—Distribution map of *Allocormodes*: *A. maculipennis* [■]; *A. maynei* [▲]; *A. nigris* [●]; *A. nigris* melanistic males [● with white center].

Table 1. *Allocormodes* cladistic character data matrix. This table presents cladistic codings of 35 characters for three outgroup and eleven ingroup taxa. Data in square brackets [0 1] represent polymorphisms. Question marks (?) represent character states that were unobtainable or uncertain (i.e., missing). See 'Cladistic analysis' for discussion.

	character number																																		
taxon	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**
Albardia furcata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Amoea vacua	1	0	0	0	0	0	0	2	0	0	[0 1]	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	[1 2]	[0 1]	0	0	0	0	?
Paramelambrotus whiteheadi	1	0	0	0	1	0	?	2	1	1	0	0	0	3	0	0	0	?	1	0	3	0	1	0	2	0	0	?	0	1	3	3	2	?	1
Allocormodes albus	1	0	0	1	1	1	1	2	0	1	0	0	0	2	0	1	?	1	1	1	?	?	1	0	0	0	?	1	1	1	2	1	0	1	?
Allocormodes inconspicuus	1	0	0	1	1	0	0	1	1	1	0	0	0	[1 2]	0	0	0	0	0	0	3	0	1	0	1	0	0	1	1	0	3	1	0	1	1
Allocormodes intractabilis	1	0	0	1	1	0	0	2	1	1	0	0	0	2	0	0	0	0	0	1	2	[3 4]	1	0	0	0	0	1	1	0	3	1	0	1	1
Allocormodes junodi	1	0	0	1	1	1	1	1	1	1	0	0	0	2	0	0	0	0	0	0	3	0	1	0	0	0	0	0	1	0	3	[1 2]	1	1	2
Allocormodes kolbei	1	1	1	2	2	1	0	1	1	1	0	0	0	2	0	0	1	0	1	1	2	3	1	0	1	1	1	2	1	0	2	1	0	1	1
Allocormodes lefebvrei	2	1	1	2	2	1	0	2	1	1	0	0	0	2	1	0	1	0	1	1	2	3	1	0	1	1	1	2	2	1	3	1	0	1	1
Allocormodes maculipennis	1	0	0	1	1	0	1	1	1	2	1	0	0	1	0	1	0	0	0	0	3	2	1	1	1	0	0	1	1	0	3	1	0	1	2
Allocormodes maynei	1	0	0	1	1	1	0	1	1	1	1	0	0	1	0	1	?	0	0	0	?	?	2	0	1	0	?	1	1	0	3	2	0	1	?
Allocormodes micheli	1	0	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	3	1	1	0	1	0	1	1	1	0	3	1	0	1	1
Allocormodes nigris	1	0	0	1	1	0	0	1	1	1	1	1	2	1	0	0	0	0	0	0	3	1	1	0	1	0	0	?	1	0	3	1	0	1	2
Allocormodes nigristigma	1	0	0	1	1	0	1	1	1	1	0	1	2	1	0	0	0	0	0	0	3	2	1	0	1	0	0	1	1	0	4	1	0	1	[1 2]

Table 2. List of unambiguous apomorphies, by branch. Syn- and autapomorphies obtained in the cladistic analysis, as optimized by PAUP* onto the final topology (A1 Fig. 1). Consistency index value is given in square brackets following each character change. Ambiguous changes are not reported.

branch	# changes	apomorphic character change(s)
node 1 → Albardia furcata	3	char. 1: 1→0 [1.000]; char. 8: 2→0 [0.667]; char. 14: 2→0 [1.000]
node 1 → Amoea vacua	2	char. 27: 0→3 [0.667], char. 34: 1→0 [1.000]
node 1 → node 2	4	char. 5: 0→1 [1.000]; char. 9: 0→1 [0.500]; char. 10: 0→1 [1.000]; char. 23: 0→1 [1.000]
node 2 → Paramelambrotus whiteheadi	3	char. 14: 2→3 [1.000]; char. 25: 0→2 [0.500]; char. 33: 0→2 [1.000]
node 2 → node 3	1	char. 4: 0→1 [1.000]
node 3 → node 10	3	char. 20: 0→1 [1.000]; char. 21: 3→2 [1.000]; char. 22: 0→3 [1.000]
node 10 → node 11	1	char. 6: 0→1 [0.333]
node 11 → Allocormode albus	4	char. 7: 0→1 [0.250]; char. 9: 1→0 [0.500]; char. 16: 0→1 [0.500]; char. 18: 0→1 [1.000]
node 11 → node 12	7	char. 2: 0→1 [1.000]; char. 3: 0→1 [1.000]; char. 4: 1→2 [1.000]; char. 5: 1→2 [1.000]; char. 25: 0→1 [0.500]; char. 26: 0→1 [1.000]; char. 28:
node 12 → Allocormodes kolbei	1	char. 8: 2→1 [0.667]
node 12 → Allocormodes lefebvrei	3	char. 1: 1→2 [1.000]; char. 15: 0→1 [1.000]; char. 29: 1→2 [0.667]
node 3 → node 4	1	char. 8: 2→1 [0.667]
node 4 → node 5	2	char. 7: 0→1 [0.250]; char. 35: 1→2 [0.667]
node 5 → Allocormodes junodi	3	char. 6: 0→1 [0.333]; char. 28: 1→0 [0.667]; char. 33: 0→1 [1.000]
node 5 → node 6	2	char. 14: 2→1 [1.000]; char. 22: 0→2 [1.000]
node 6 → node 7	1	char. 16: 0→1 [0.500]
node 7 → Allocormodes maculipennis	2	char. 10: 1→2 [1.000]; char. 24: 0→1 [1.000]
node 7 → Allocormodes maynei	4	char. 6: 0→1 [0.333]; char. 7: 1→0 [0.250]; char. 23: 1→2 [1.000]; char. 32: 1→2 [1.000]
node 6 → node 8	2	char. 12: 0→1 [1.000]; char. 13: 0→2 [1.000]
node 8 → node 9	1	char. 22: 2→1 [1.000]
node 9 → Allocormodes micheli	3	char. 13: 2→1 [1.000]; char. 27: 0→1 [0.667]; char. 35: 2→1 [0.667]
node 9 → Allocormodes nigris	1	char. 7: 1→0 [0.250]
node 8 → Allocormodes nigristigma	1	char. 31: 3→4 [0.800]

Table 3. List of character state changes, by character. Character states transformations as optimized by PAUP* on the topology obtained in the cladistic analysis (13 Fig. 1) are presented here. Optimizations are provided in the format [node#: ancestral state→derived state node# OR node#: ancestral state→state of terminal taxon]. Node numbers correspond to those found on A1 Fig. 1. Both unambiguous (→) and ambiguous (-->>) character state changes are provided.

char#	CI	steps	state transformation(s)
1	1.000	2	node 1: 1 → 0 Albardia furcata; node 12: 1 → 2 Allocormodes lefebvrei
2	1.000	1	node 11: 0 → 1 node 12
3	1.000	1	node 11: 0 → 1 node 12
4	1.000	2	node 2: 0 → 1 node 3; node 11: 1 → 2 node 12
5	1.000	2	node 1: 0 → 1 node 2; node 11: 1 → 2 node 12
6	1.000	3	node 12: 0 → 1 node 11; node 5: 0 → 1 Allocormodes junodi; node 7: 0 → 1 Allocormodes maynei
7	0.250	4	node 11: 0 → 1 Allocormodes albus; node 4: 0 → 1 node 5; node 7: 1 → 0 Allocormodes maynei; node 9: 1 → 0 Allocormodes nigris
8	0.667	3	node 2: 2 → 0 Albardia furcata; node 12: 2 → 1 Allocormodes kolbei; node 3: 2 → 1 node 4
9	0.500	2	node 1: 0 → 1 node 2; node 11: 1 → 0 Allocormodes albus
10	1.000	2	node 1: 0 → 1 node 2; node 7: 1 → 2 Allocormodes maculipennis
11	0.500	2	node 5: 0 -->> 1 node 6; node 8: 1 -->> 0 Allocormodes nigristigma
12	1.000	1	node 6: 0 → 1 node 8
13	1.000	2	node 6: 0 → 2 node 8; node 9: 2 → 1 Allocormodes micheli
14	1.000	3	node 1: 2 → 0 Albardia furcata; node 2: 2 → 3 Paramelambrotus whiteheadi; node 5: 2 → 1 node 6
15	1.000	1	node 12: 0 → 1 Allocormodes lefebvrei
16	0.500	2	node 11: 0 → 1 Allocormodes albus; node 6: 0 → 1 node 7
17	1.000	1	node 10: 0 -->> 1 node 11:
18	1.000	1	node 11: 0 → 1 Allocormodes albus
19	0.333	3	node 1: 0 -->> 1 Albardia furcata; node 2: 0 -->> 1 Paramelambrotus whiteheadi; node 10: 0 -->> 1 node 11:
20	1.000	1	node 3: 0 → 1 node 10
21	1.000	3	node 1: 0 -->> 1 Albardia furcata; node 1: 0 -->> 3 node 2; node 3: 3 → 2 node 10
22	1.000	3	node 3: 0 → 3 node 10; node 5: 0 → 2 node 6; node 8: 2 → 1 node 9
23	1.000	2	node 1: 0 → 1 node 2; node 7: 1 → 2 Allocormodes maynei
24	1.000	1	node 7: 0 → 1 Allocormodes maculipennis
25	0.500	4	node 2: 1 → 2 Paramelambrotus whiteheadi; node 11: 0 → 1 node 12; node 3: 0 -->> 1 node 4; node 22 1 -->> 0 Allocormodes junodi
26	1.000	1	node 11: 0 → 1 node 12
27	0.667	3	node 1: 0 → 3 Amoea vacua; node 10: 0 -->> 1 node 11; node 9: 0 → 1 Allocormodes micheli
28	0.667	3	node 1: 0 -->> 1 node 2; node 11: 1 → 2 node 12; node 5: 1 → 0 Allocormodes junodi
29	0.667	3	node 1: 0 -->> {12} Amoea vacua; node 2: 0 -->> 1 node 3; node 12: 1 → 2 Allocormodes lefebvrei
30	0.333	3	node 2: 1 -->> 0 node 3; node 10: 0 -->> 1 node 11; node 12: 1 -->> 0 Allocormodes kolbei
31	0.800	5	node 1: 0 -->> 1 Albardia furcata; node 1: 0 -->> 3 node 2; node 10: 3 -->> 2 node 11; node 12: 2 -->> 3 Allocormodes lefebvrei; node 8: 3 → 4 Allocormodes nigristigma
32	1.000	3	node 1: 0 -->> 1 node 2; node 2: 1 -->> 3 Paramelambrotus whiteheadi; node 7: 1 → 2 Allocormodes maynei
33	1.000	2	node 2: 0 → 2 Paramelambrotus whiteheadi; node 5: 0 → 1 Allocormodes junodi
34	1.000	1	node 1: 1 → 0 Amoea vacua
35	0.667	3	node 1: 0 -->> 1 node 2; node 4: 1 → 2 node 5; node 9: 2 → 1 Allocormodes micheli

APPENDIX 2

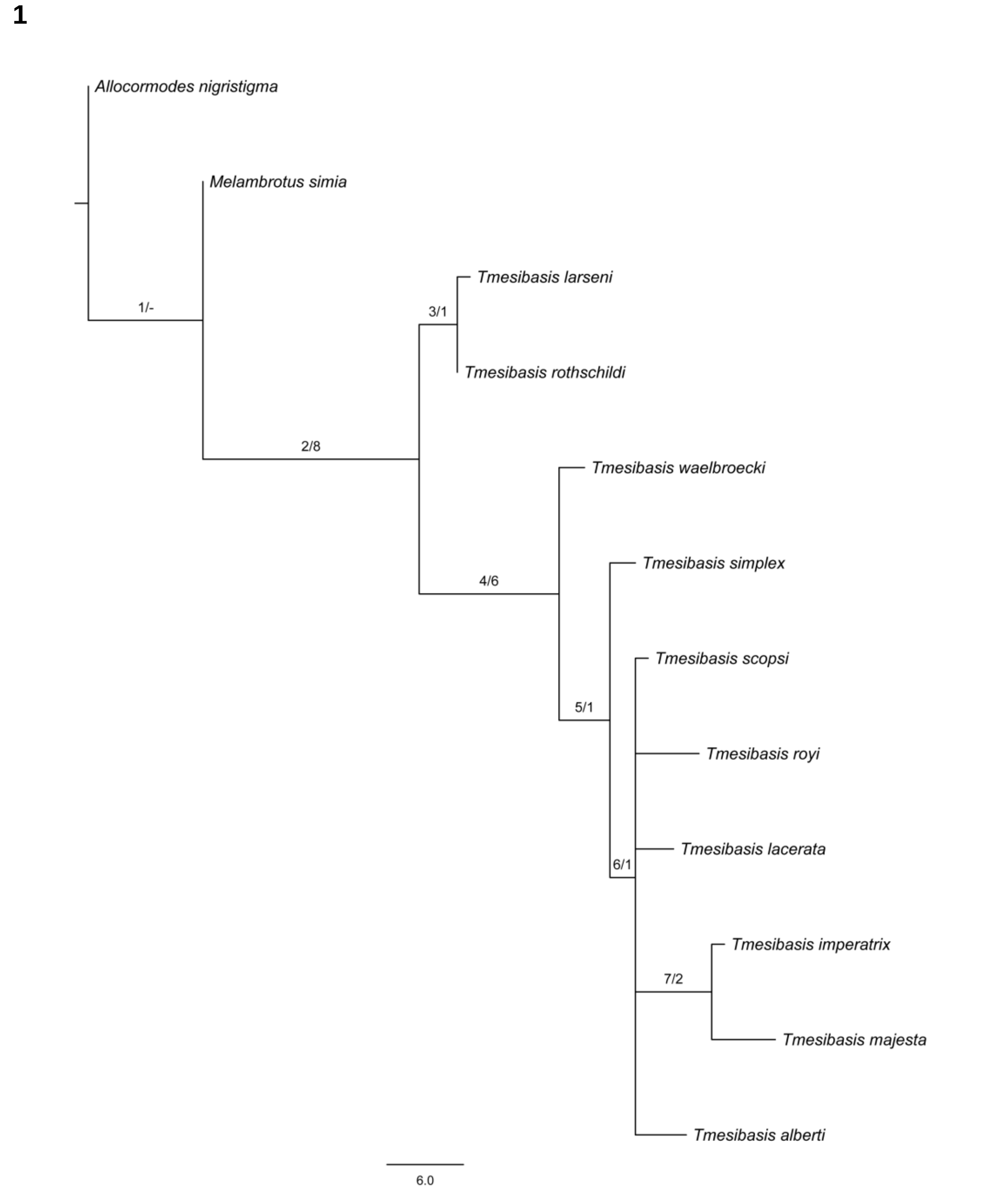
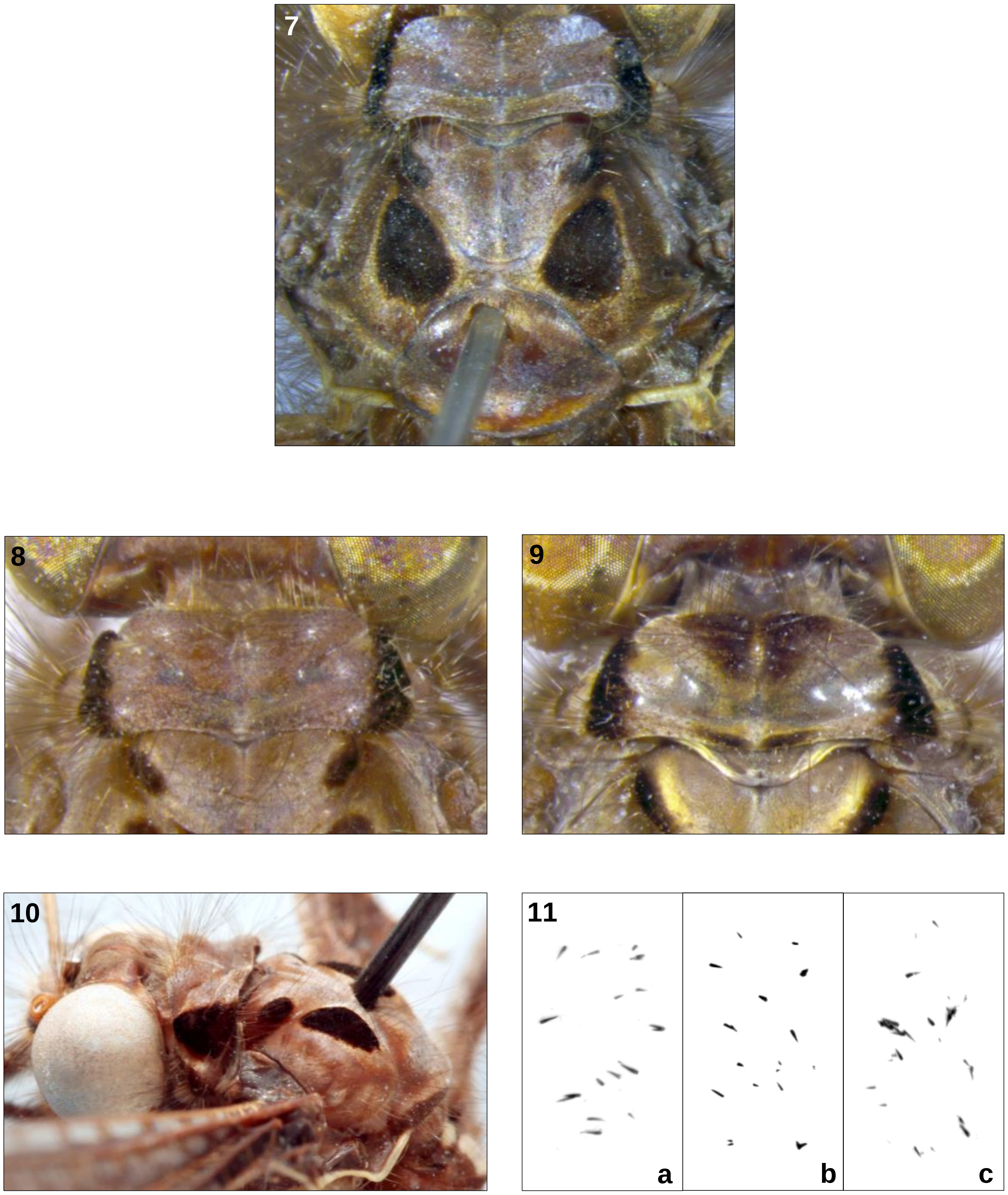
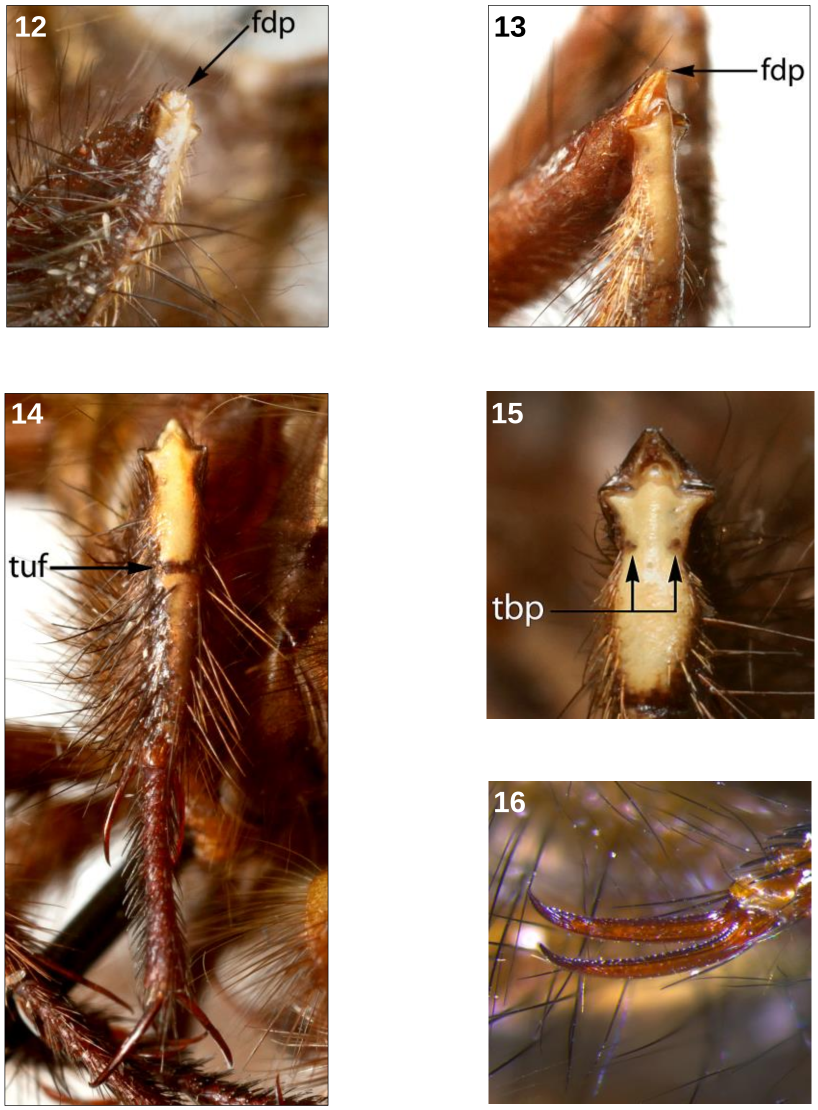


Fig. 1.—Phylogram of *Tmesibasis* species. This topology is a strict consensus two trees generated from TNT and PAUP* analysis of morphological characters. Outgroup taxa = *Allocormodes nigristigma*, *Melambrotus simia*; # ingroup taxa = 10; # characters = 39; length = 76; C. I. = 0.8684; R. I. = 0.8507. Numbers above branches (e.g., 2/8) indicate the number of the adjacent (distad) node followed by Bremer support value for that node. Node numbers correspond to those given in the character state change list (see A2 Table 3). For a list of node synapomorphies and terminal taxon autapomorphies see A2 Table 2 and individual taxon descriptions.

Figs. 2–6.—Eyes and antennae of outgroup and *Tmesibasis*. 2.—Eye entire, without transverse depression (*Melambrotus papio*: JRJ_00696). 3.—Eye entire, but with transverse depression (*T. alberti*: JRJ_01272). 4.—Club developed, color brown (*T. larseni*: JRJ_01306) The club in dry specimens is slightly flattened and broadened, and in life would be inflated and slightly narrower. 5.—Club reduced, color brown (*T. waelbroecki*: JRJ_01259). 6.—Club reduced, apical flagellomeres yellow (*T. majesta*: JRJ_01232).



Figs. 7–11.—Prothorax, mesothorax and velvety spots of *Tmesibasis*. 7.—Prothorax and mesothorax with well-developed velvety spots, dorsal (*T. waelbroecki*: JRJ_01250). 8.—Prothorax with anterior flange lobes and posterior flange evenly brown dorsal coloration (*T. waelbroecki*: JRJ_01037). 9.—Prothorax with prescutum and scutellum mesally darkened (*T. majesta*: JRJ_01234). 10.—Thoracic velvety stripe, dorsolateral view (*T. waelbroecki*: JRJ_01238). 11.—Velvety spot spicules (a: *T. scopsi*: JRJ_01027; b: *T. majesta*: JRJ_01256; c: *T. waelbroecki*: JRJ_01258); images were edited in gray scale to eliminate glare from light source.



Figs. 12–16.—Leg features of *Tmesibasis*. 12.—Femur apex, dorsoapical process absent, oblique view (*T. rothschildi*: JRJ_01022). 13.—Femur apex, dorsoapical process present, oblique view (*T. waelbroecki*: JRJ_01238). 14.—Tibia upper fascia (*T. royi*: JRJ_01237). 15.—Tibia basidorsal pores (*T. imperatrix*: JRJ_01261). 16.—Tarsal claw, ventrolateral view, showing ventral carinae and bumps (*T. scopsi*: JRJ_01245). Abbreviations: *fdp* = femur dorsoapical process; *tbp* = tibia basidorsal pore; *tuf* = tibia upper fascia.

17

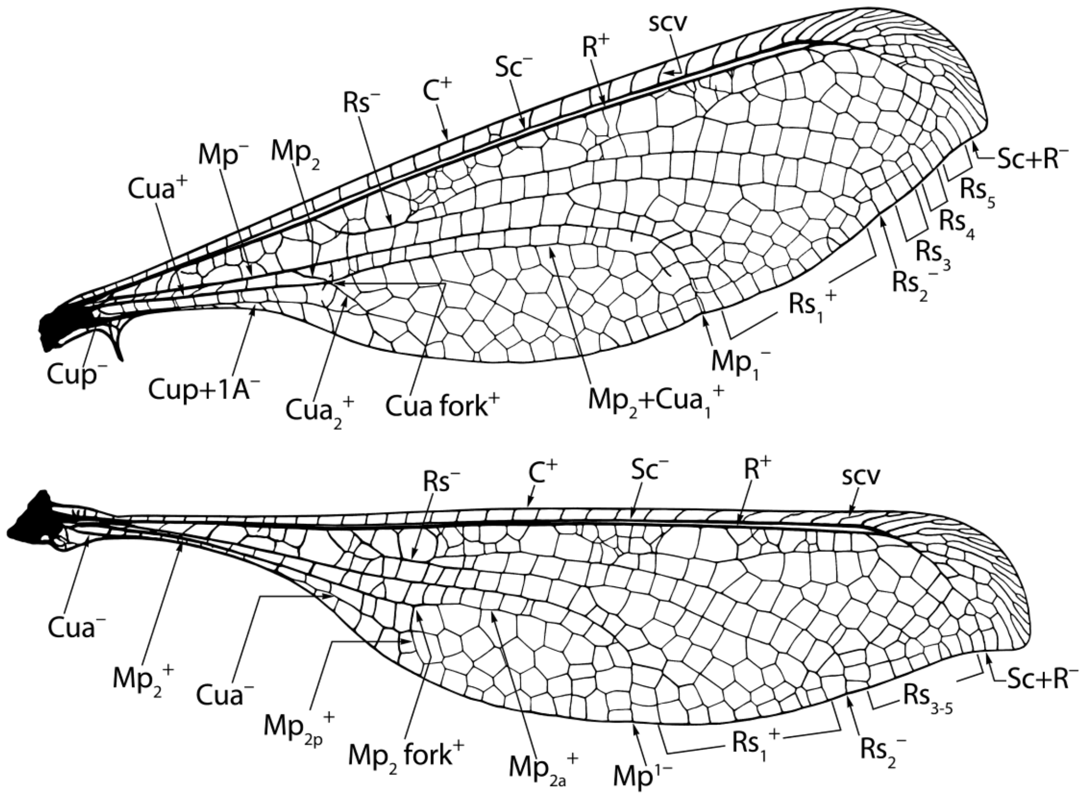
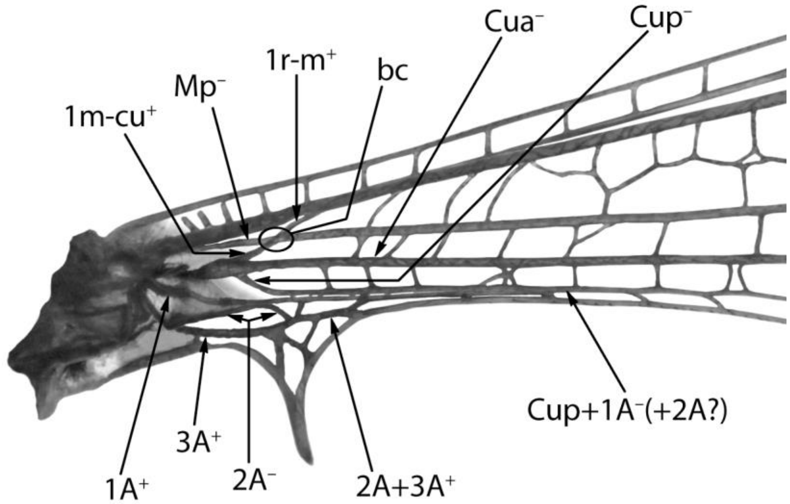
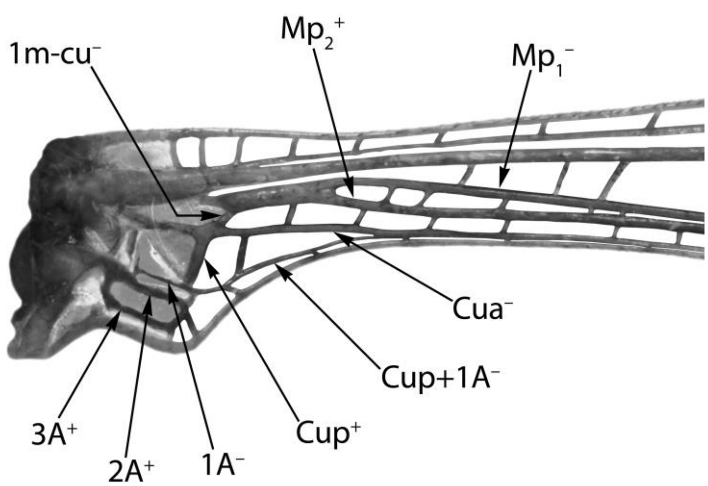


Fig. 17.—Wing venation of *Tmesibasis imperatrix* (♀, JRJ_01006: crimping and bending at anterior margin of HW base are artifacts of spreading); major veins are indicated as either convex (+) or concave (–) in dorsal view. Membrane patterning has been edited out to emphasize venation. Abbreviations: *1A* = first anal vein; *C* = costa; *Cua* = cubitus anterior; *Cup* = cubitus posterior; *Mp* = media posterior; *Rs* = radial sector; *R* = radius; *Sc* = subcosta; *scv* = subcostal veinlet.

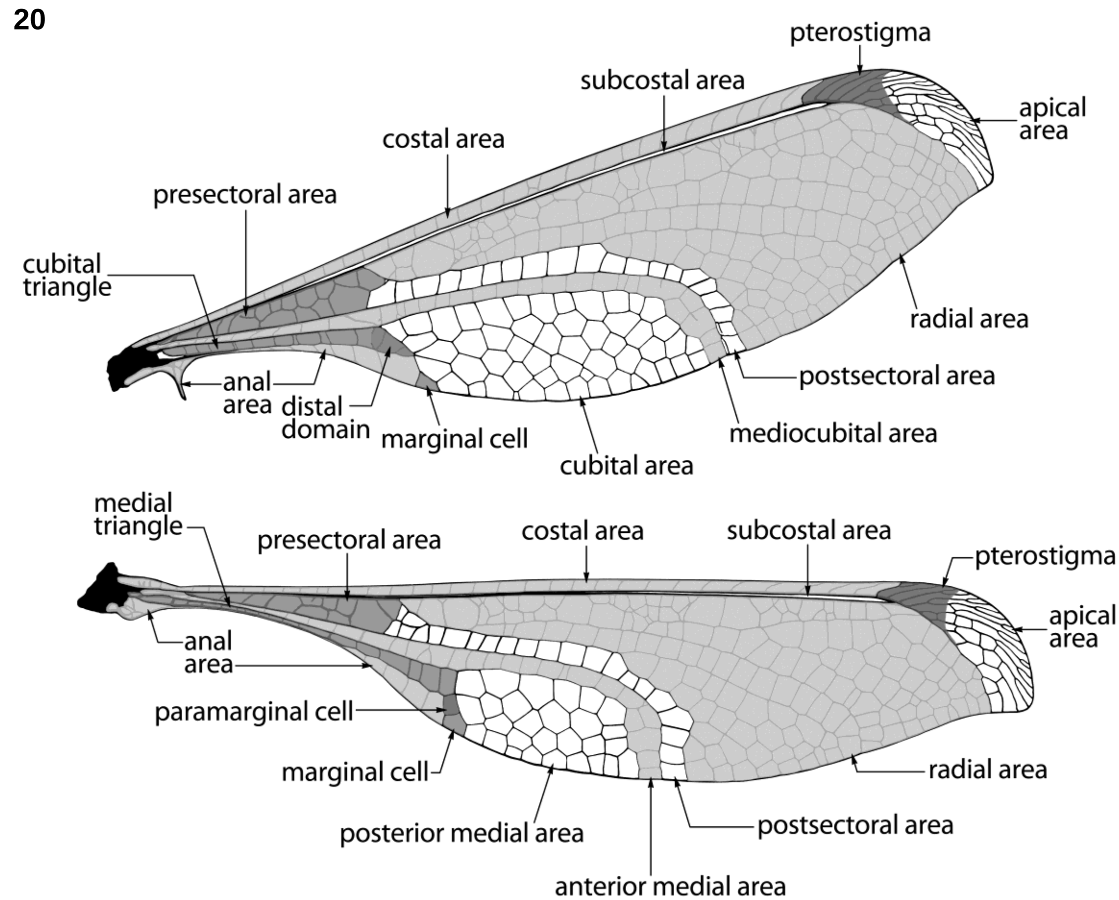
18



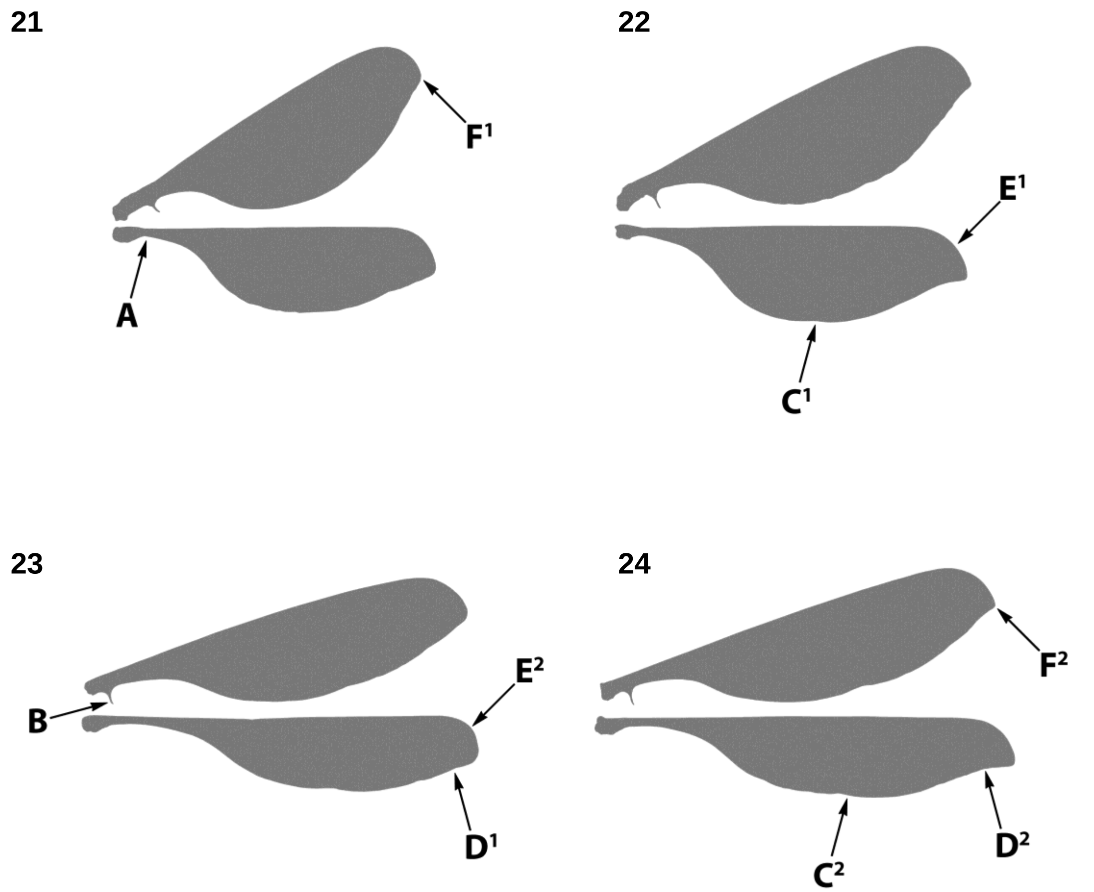
19



Figs. 18–19.—Basal wing venation of *Tmesibasis*. 18.—Forewing (*T. imperatrix* ♀, JRJ_01006). 19.—Hind wing (*T. waelbroecki* ♂, JRJ_01032). Membrane patterning has been edited out to emphasize venation. Not to same scale. Abbreviations: *1A* = first anal vein; *2A* = second anal vein; *3A* = third anal vein; *bc* = basal chiasma; *Cua* = cubitus anterior; *1m-cu* = first medio-cubital crossvein; *Cup* = cubitus posterior; *Mp* = media posterior; *1r-m* = first radius-media crossvein.

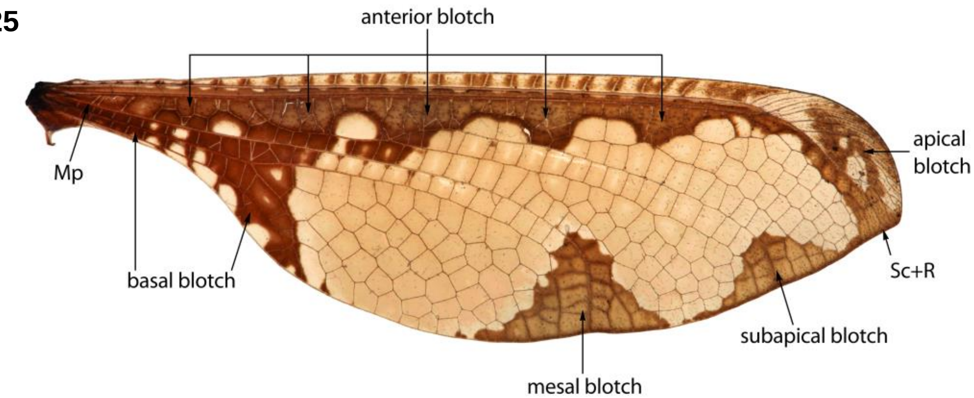


Figs. 20.—Wing areas in *Tmesibasis imperatrix* (♀, JRJ_01006).

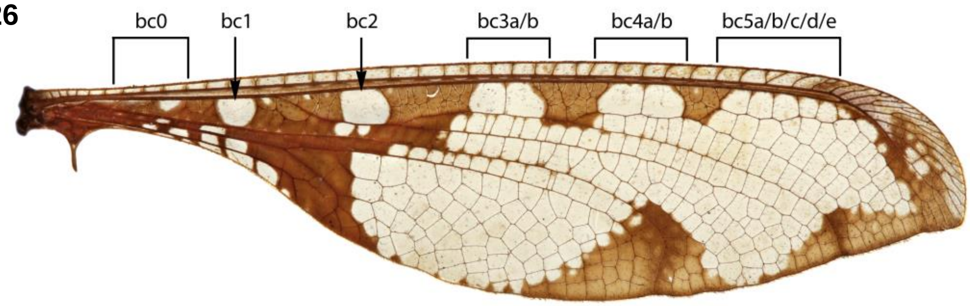


Figs. 21–24.—Wing shape attributes in *Tmesibasis*. 21.—*T. rothschildi* ♂ (JRJ_01021). 22.—*T. waelbroecki* ♂ (JRJ_01036). 23.—*T. majesta* ♂ (JRJ_01232). 24.—*T. majesta* ♀ (JRJ_01234). Key.—A: wing base narrowed; B: anal process narrow and elongate; C^1: wing broad near midpoint relative to wing length; C^2: wing narrow near midpoint relative to wing length; D^1: subapical hind margin weakly falcate; D^2: subapical hind margin strongly falcate; E^1: apical area broadest mesally and distal margin weakly curved; E^2: apical area broadest anteriorly and distal margin strongly curved; F^1: apical angle rounded; F^2: apical angle sharp. Wings not to same scale.

25



26



Figs. 25–28.—Forewing features in *Tmesibasis*. 25.—Wing blotches (*T. lacerata* ♂, JRJ_01013, anal process artificially bent). The anterior and basal blotches are separated by Mp/Mp^{1} in the FW and Mp^{1} in the HW; the apical blotch includes all pigment within the apical area (distad of Sc+R). 26.—Blyzocyte sets (*T. alberti* ♀, JRJ_01004). Blyzocyte 0, when present, varies somewhat in position, as indicated by the span. Sets 3–5 often vary in the number of constituent cells, as indicated by letters after the cell set number. 27.—Anal process subacuminate, lateral margins both yellow, terminal cell reaching apex of process (*T. rothschildi*, JRJ_01271). 28.—Anal process acuminate, proximal margin dark and distal margin yellow, terminal cell closing well before process apex (*T. majesta* ♀, JRJ_01234). Abbreviations: *bc* = blyzocyte/blyzocyte set.

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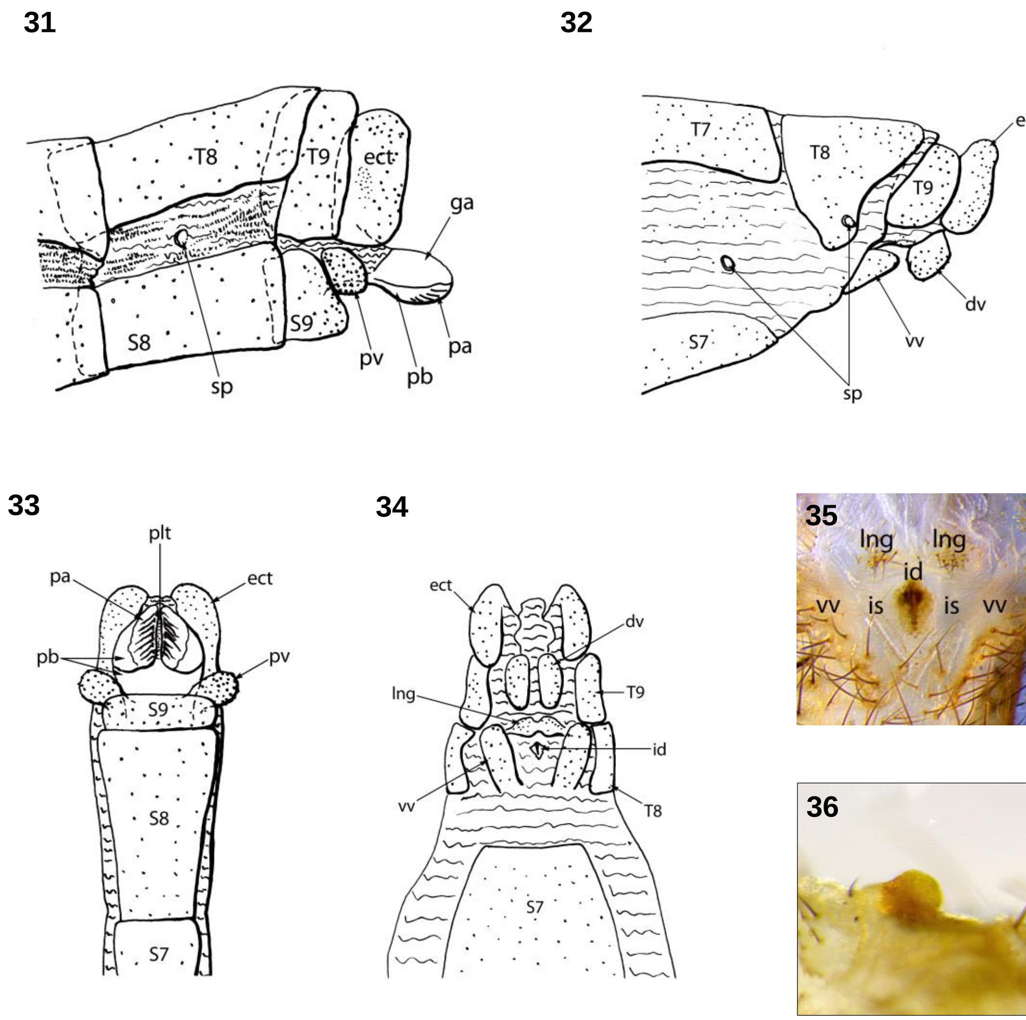
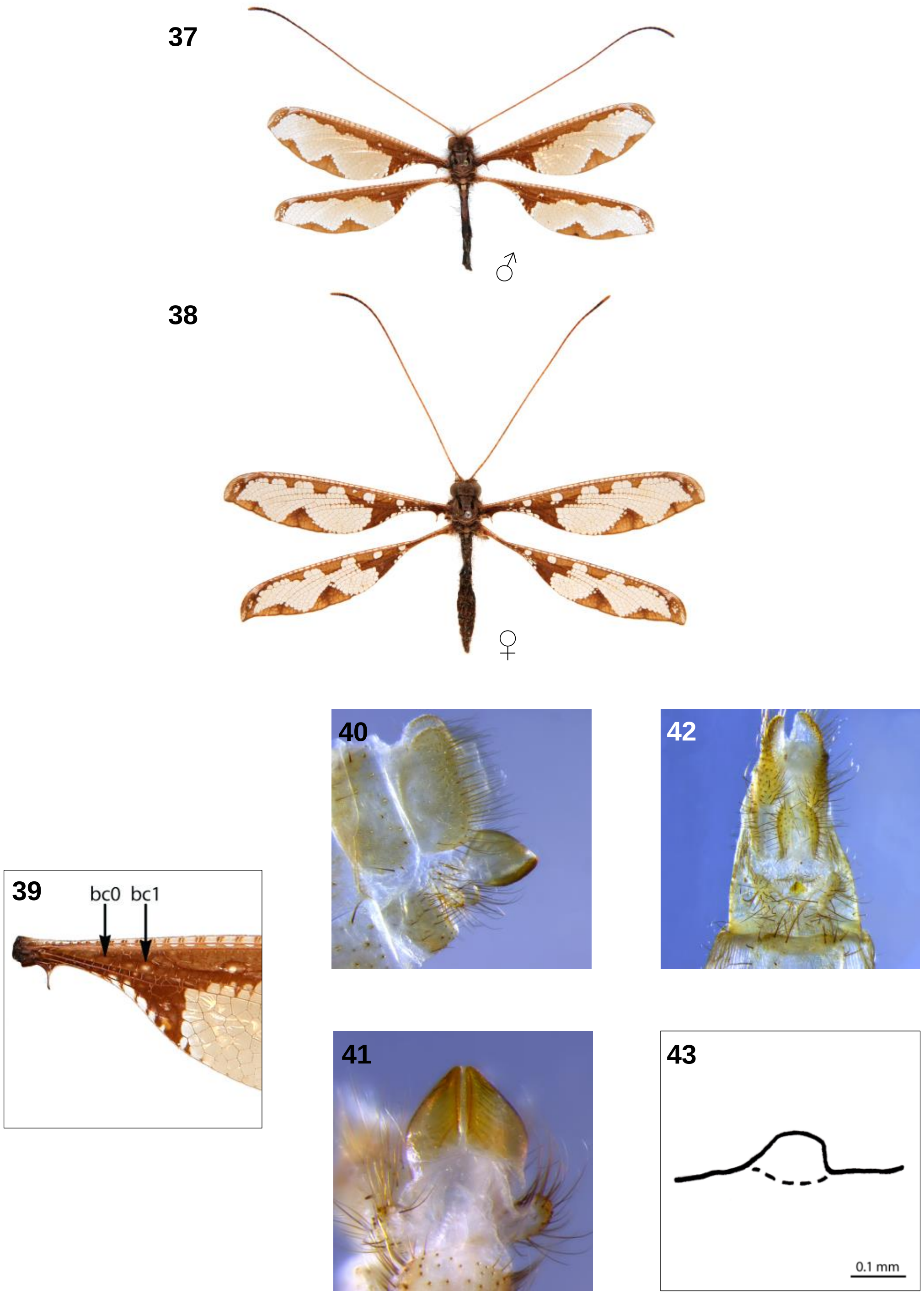
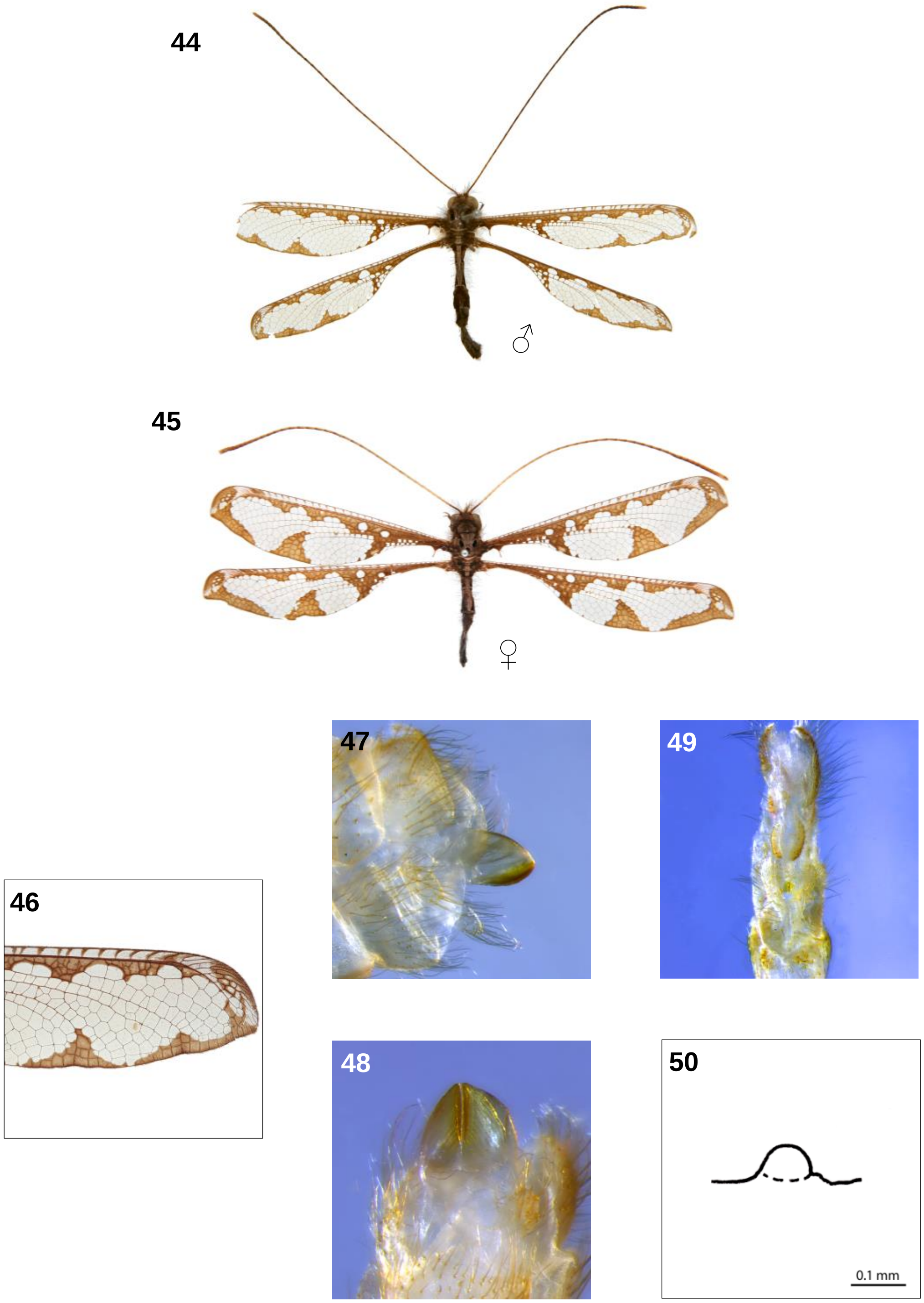
Figs. 29–30.—Live habitus images of *Tmesibasis* species; note positions of antennae, legs and wings, and colors and patterns of antennae, thorax, wings, and abdomen. 29.—*T. lacerata* ♀, Tlopi camp, Marakele National Park, South Africa. 30.—*T. scopsi* ♀, Gorongosa National Park, Mozambique.



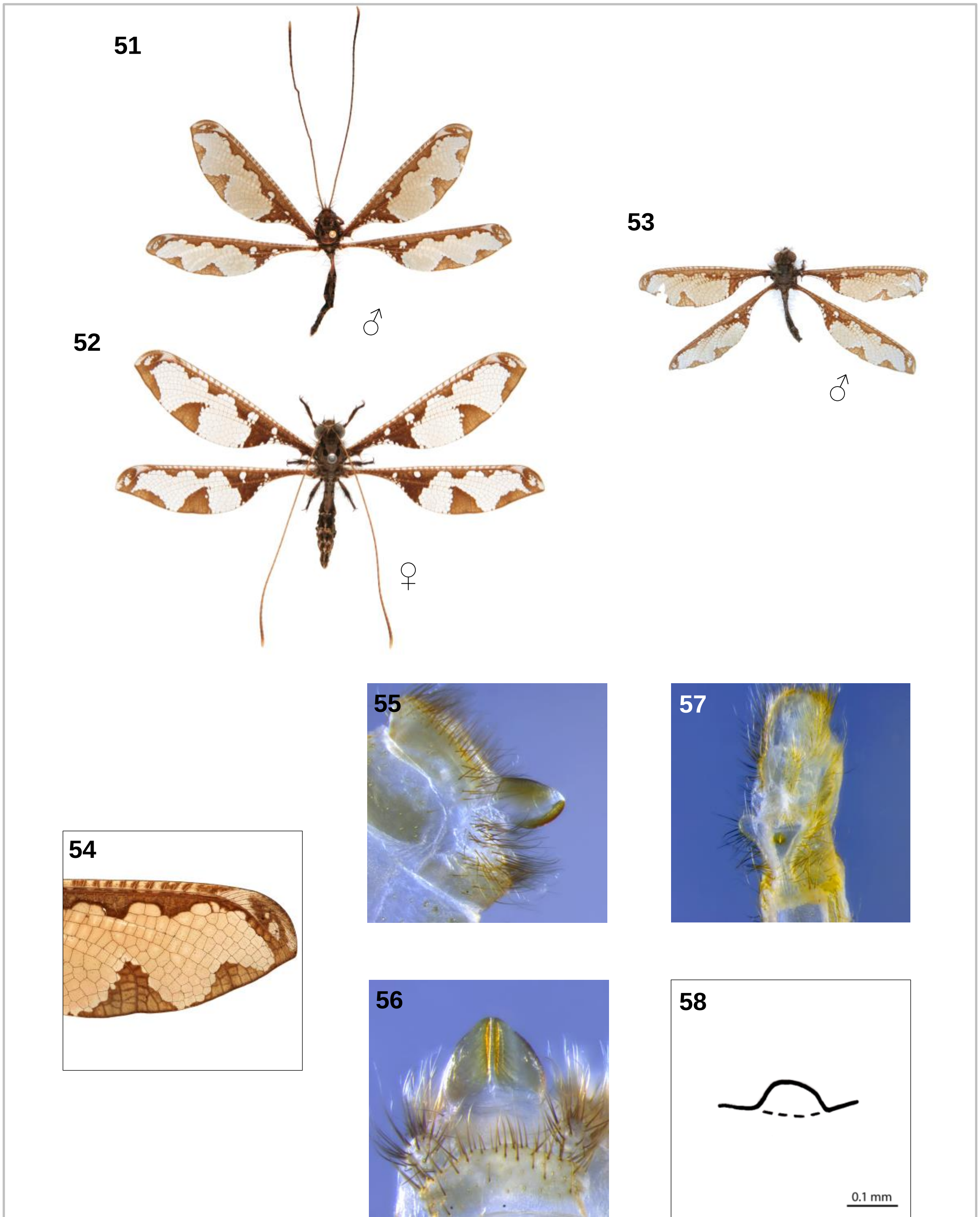
Figs. 31–36.—Abdomens and terminalia of *Tmesibasis*. 31.—Apex of abdomen, ♂, left lateral, GPC fully everted (*T. alberti*, JRJ_01243). 32.—Apex of abdomen, ♀, left lateral (*T. waelbroecki*, JRJ_01038). 33.—Apex of abdomen, ♂, ventral, GPC partially everted (*T. alberti*, JRJ_01243). 34.—Apex of abdomen, ♀, ventral (*T. waelbroecki*, JRJ_01038). 35.—Interdental space, with adjacent structures, ♀, ventral (*T. majesta*, JRJ_01234). 36.—Interdens, ♀, left lateral view (*T. alberti*, JRJ_01004). Abbreviations: *dv* = distivalve; *ect* = ectoproct; *ga* = gonarcus; *id* = interdens; *is* = interdental space; *lng* = linguella; *plt* = pelta; *pa* = paramere; *pb* = base of paramere; *pv* = pulvinus; *S* = sternite; *sp* = spiracle; *T* = tergite; *vv* = ventrovalve.



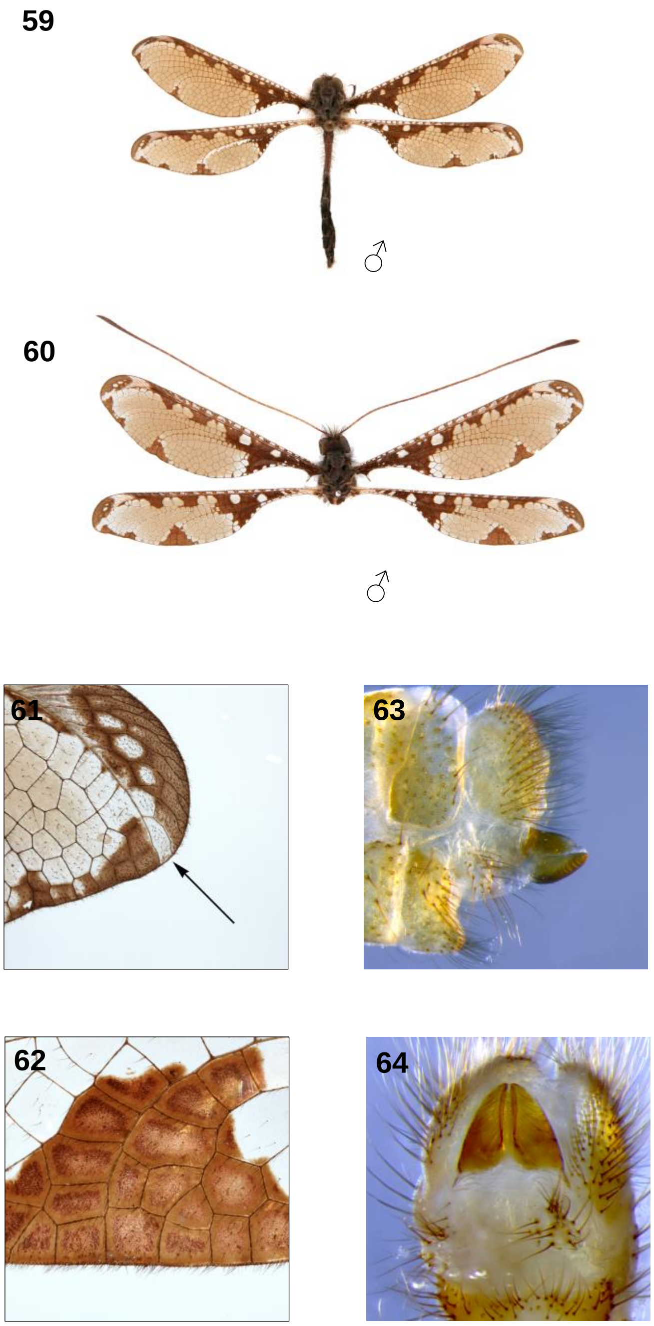
Figs. 37–43.—*Tmesibasis alberti*. 37.—Habitus, spread, holotype ♂, dorsal, RMCA, JRJ_01240. 38.—Habitus, spread, ♀, dorsal, JRJ_01004. 39.—FW base showing completely or nearly completely pigmented blyzocytes, ♂, JRJ_01240. 40.—Abdomen apex, ♂, left lateral, JRJ_01264. 41.—Abdomen apex, ♂, ventral, JRJ_01264. 42.—Abdomen apex, ♀, ventral, JRJ_01004. 43.—Interdens, ♀, left lateral, JRJ_01004. Abbreviations: *bc* = blyzocyte.



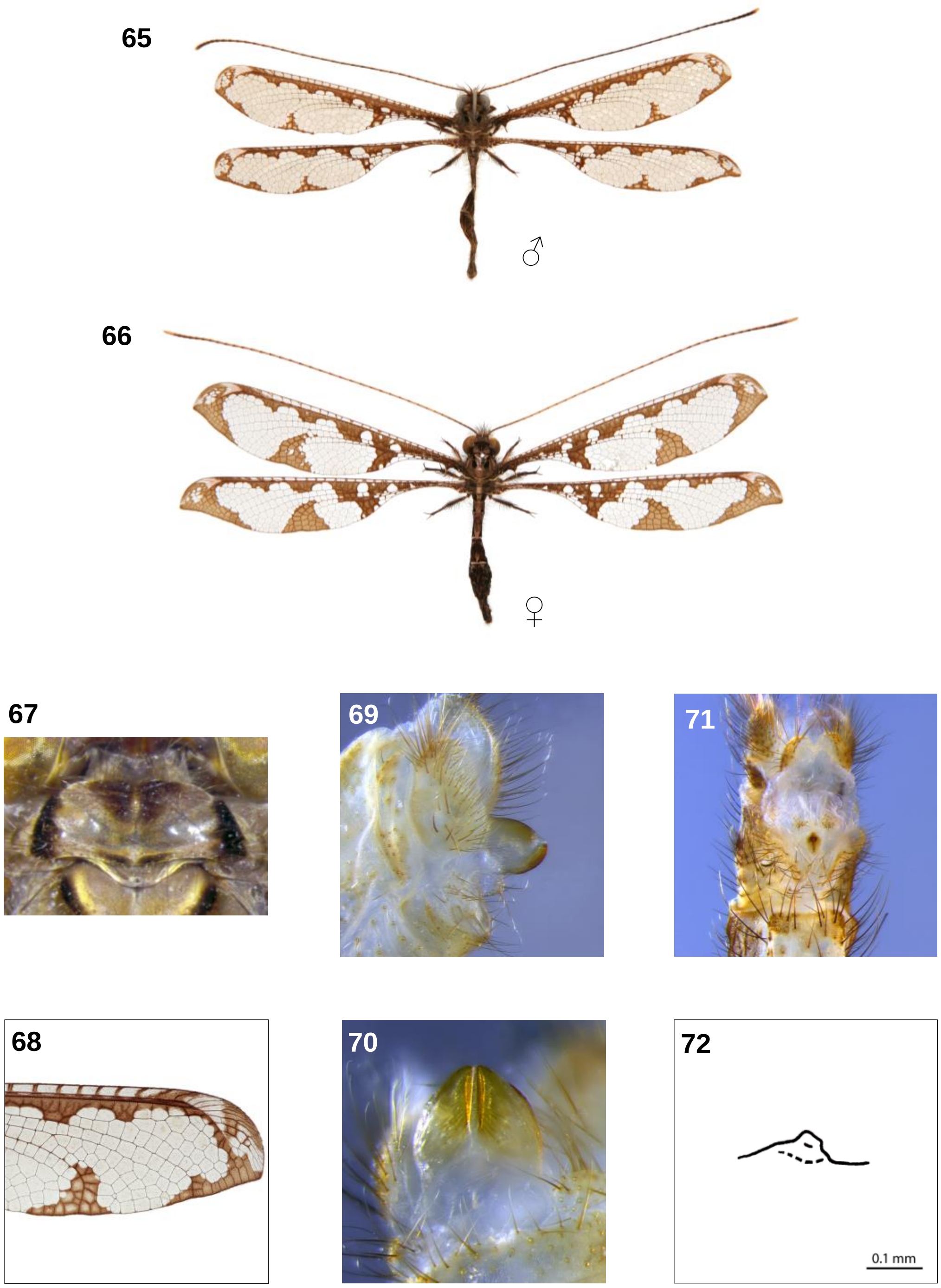
Figs. 44–50.—*Tmesibasis imperatrix*. 44.—Habitus, spread, ♂, dorsal, JRJ_01251. 45.—Habitus, spread, holotype ♀, dorsal, BMNH, JRJ_01247. 46.—FW mesal and subapical blotches, dorsal, ♂, JRJ_01251. 47.—Abdomen apex, ♂, left lateral, JRJ_01252. 48.—Abdomen apex, ♂, ventral, JRJ_01252. 49.—Abdomen apex, ♀, ventral, JRJ_01247. 50.—Interdens, ♀, left lateral, JRJ_01270.



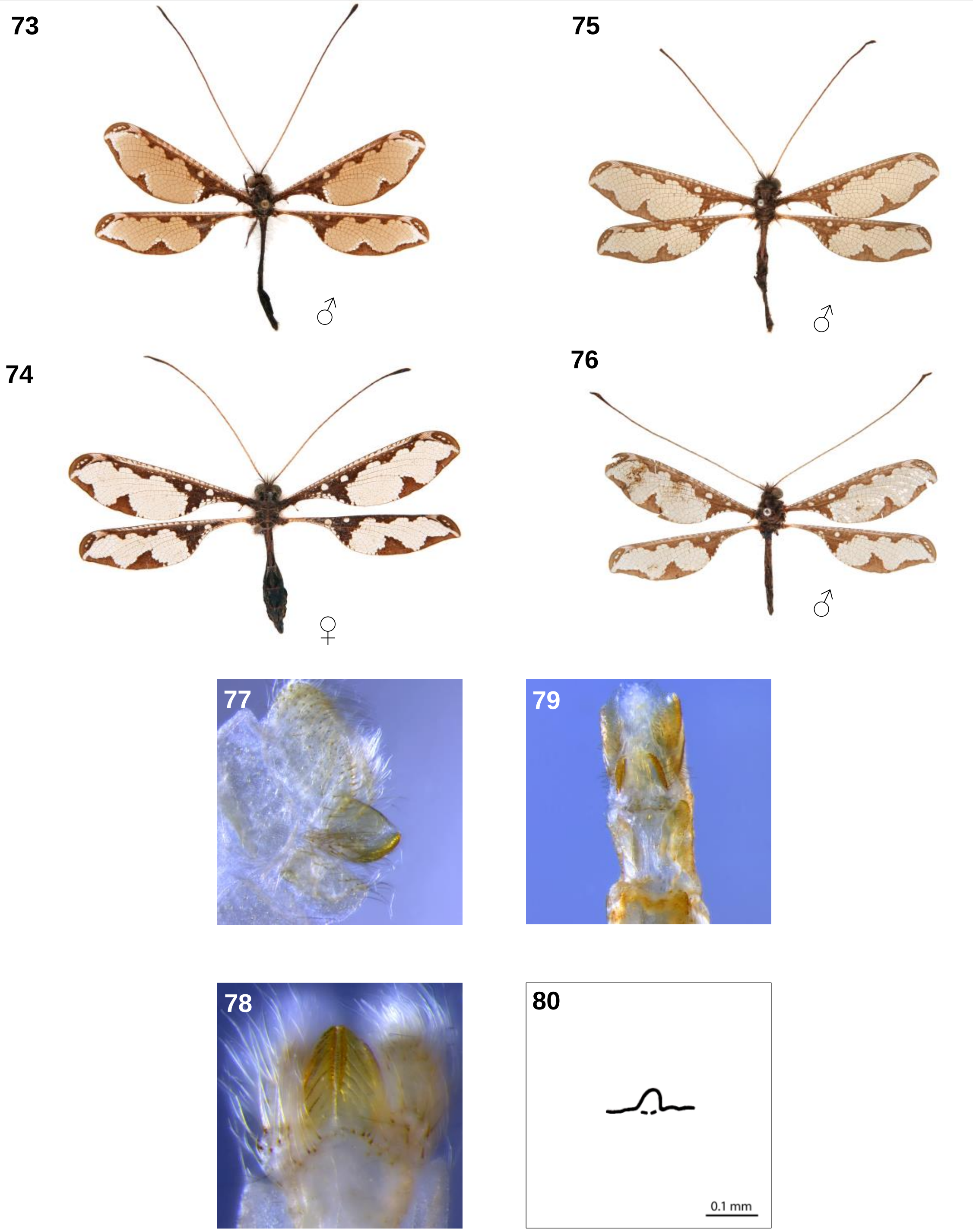
Figs. 51–58.—*Tmesibasis lacerata*. 51.—Habitus, spread, ♂, dorsal, JRJ_01013. 52.—Habitus, spread, ♀, dorsal, JRJ_01017. 53.—Habitus, spread, lectotype ♂, dorsal, MFNB, JRJ_01153. 54.—Closeup of ♂ FW posterior blotches, JRJ_01013. 55.—Abdomen apex, ♂, left lateral, JRJ_01014. 56.—Abdomen apex, ♂, ventral, JRJ_01014. 57.—Abdomen apex, ♀, ventral, JRJ_01016. 58.—Interdens, ♀, left lateral, JRJ_01005.



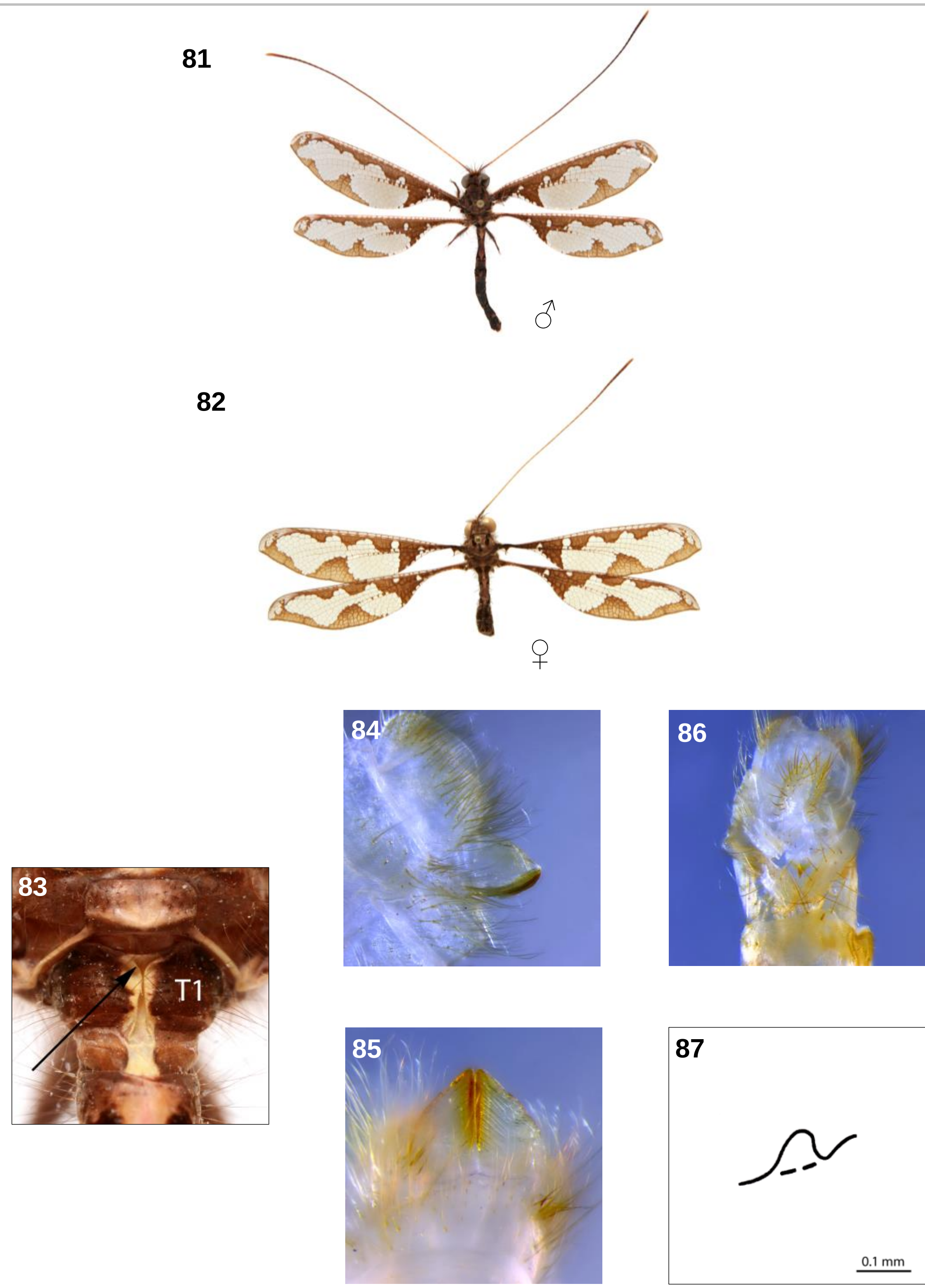
Figs. 59–64.—*Tmesibasis larseni*. 59.—Habitus, spread, ♂, dorsal, JRJ_01019. 60.—Habitus, spread, holotype ♂, dorsal, BMNH, JRJ_01306. 61.—Closeup of ♂ FW apical area, displaying posterior marginal pigment gap, JRJ_01306. 62.—Closeup of pigmented wing membranes, showing rough mesal texture (of *T. rothschildi*, nearly identical to that in *T. larseni*) JRJ_01262. 63.—Abdomen apex, ♂, left lateral, JRJ_01306. 64.—Abdomen apex, ♂, ventral, JRJ_01306.



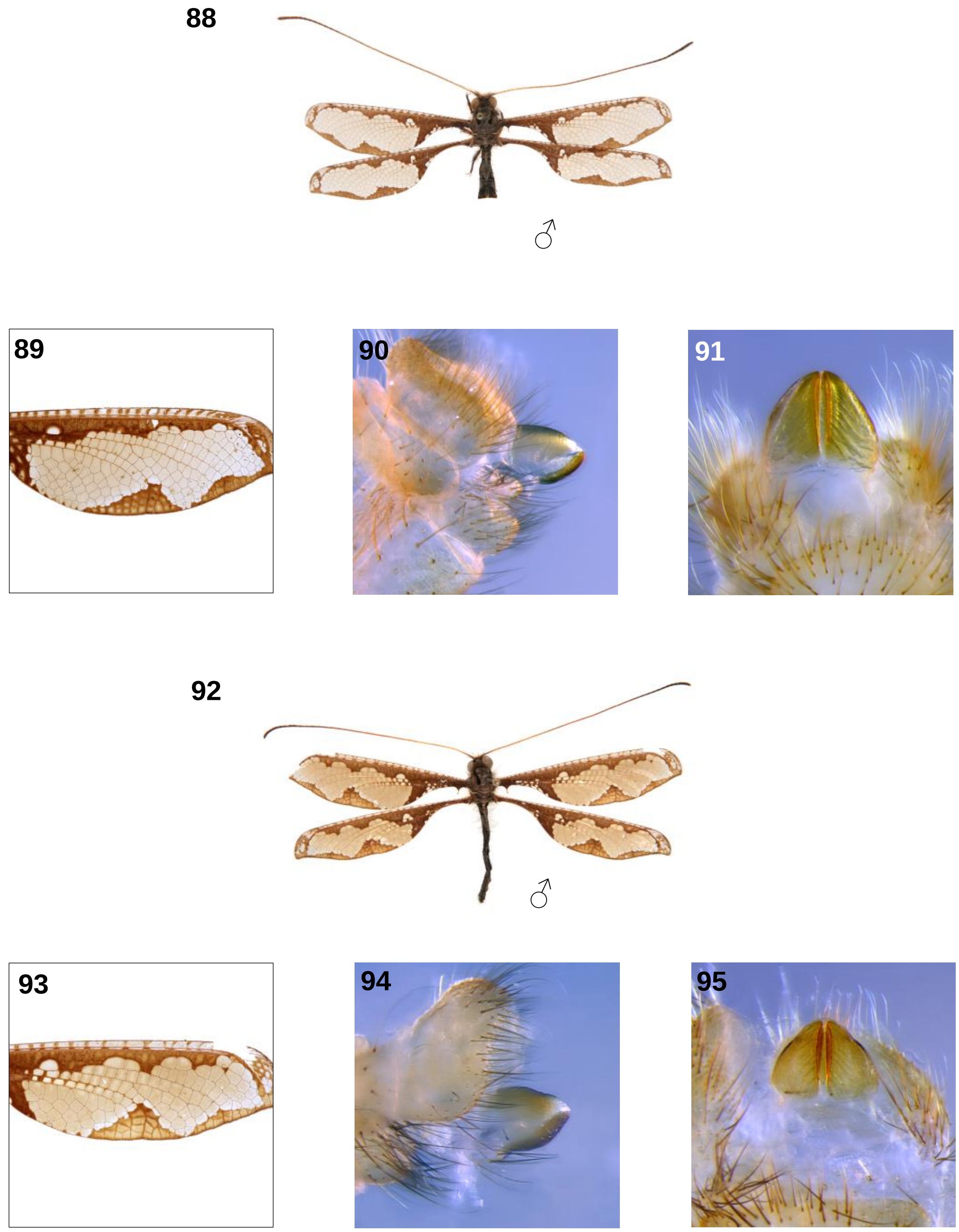
Figs. 65–72.—*Tmesibasis majesta*. 65.—Habitus, spread, ♂, dorsal, JRJ_01232. 66.—Habitus, spread, holotype ♀, dorsal, BMNH, JRJ_01234. 67.—Prothorax, dorsal, with anteromesal portions or prescutum and scutellum darkened, JRJ_01234. 68.—Closeup of ♂ FW posterior blotches, JRJ_01030. 69.—Abdomen apex, ♂, left lateral, JRJ_01030. 70.—Abdomen apex, ♂, ventral, JRJ_01030. 71.—Abdomen apex, ♀, ventral, JRJ_01234. 72.—Interdens, ♀, left lateral, JRJ_01234.



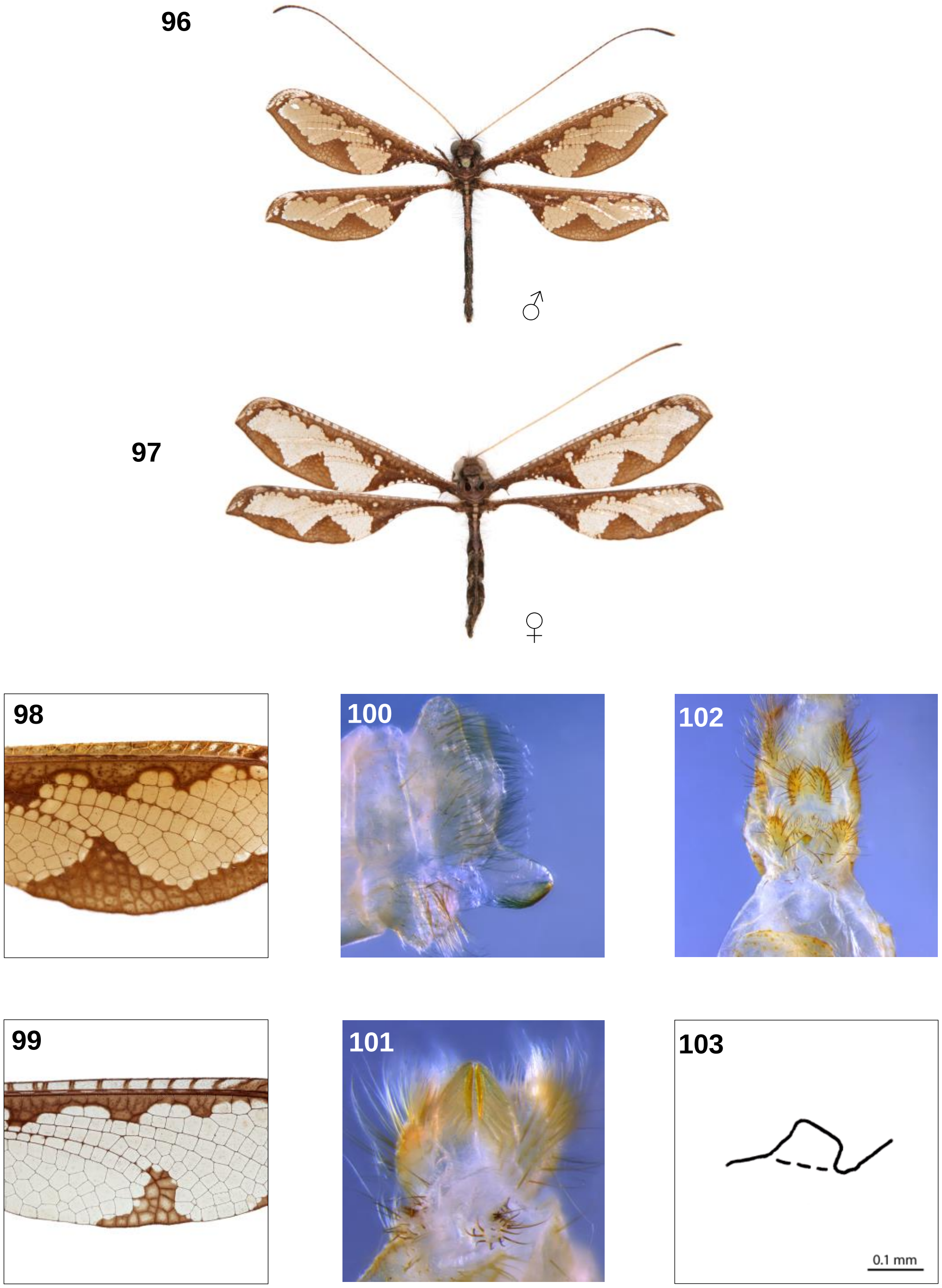
Figs. 73–80.—*Tmesibasis rothschildi*. 73.—Habitus, spread, ♂, dorsal, JRJ_01021. 74.—Habitus, spread, ♀, dorsal, JRJ_01271. 75.—Habitus, spread, lectotype ♂, dorsal, BMNH, JRJ_01248. 76.—Habitus, spread, holotype ♂ (*Tmesibasis regia*), dorsal RMCA, JRJ_01244. 77.—Abdomen apex, ♂, left lateral, JRJ_01023. 78.—Abdomen apex, ♂, ventral, JRJ_01023. 79.—Abdomen apex, ♀, ventral, JRJ_01262. 80.—Interdens, ♀, left lateral, JRJ_01262.



Figs. 81–87.—*Tmesibasis royi*. 81.—Habitus, spread, ♂, dorsal, JRJ_01025. 82.—Habitus, spread, ♀, dorsal, JRJ_01239. 83.—T1 plates and membrane, showing dark color of plates and anterior puckering of mesal membrane (arrow), JRJ_01237. 84.—Abdomen apex, ♂, left lateral, JRJ_01012. 85.—Abdomen apex, ♂, ventral, JRJ_01012. 86.—Abdomen apex, ♀, ventral, JRJ_01237. 87.—Interdens, ♀, left lateral, JRJ_01237.



Figs. 88–91.—*Tmesibasis scopsi*. Figs. 92–95.—*Tmesibasis simplex* n. sp. 88.—Habitus, spread, holotype ♂, dorsal, RMCA, JRJ_01245. 89.—Closeup FW cell rows, showing typical dense configuration, JRJ_01267. 90.—Abdomen apex, ♂, left lateral, JRJ_01026. 91.—Abdomen apex, ♂, ventral, JRJ_01026. 92.—Habitus, spread, holotype ♂, dorsal, USNM, JRJ_01031. 93.—Closeup FW cell rows, showing sparse configuration, JRJ_01031. 94.—Abdomen apex, ♂, left lateral, JRJ_01253. 95.—Abdomen apex, ♂, ventral, JRJ_01253.



Figs. 96–103.—*Tmesibasis waelbroecki*. 96.—Habitus, spread, ♂, dorsal, JRJ_01036. 97.—Habitus, spread, ♀, dorsal, JRJ_01038. 98.—Closeup costal area venation, showing irregular subcostal veinlets, JRJ_01035. 99.—Closeup of costal area venation, showing regular subcostal veinlets, for comparison (*T. majesta*, JRJ_01030). 100.—Abdomen apex, ♂, left lateral, JRJ_01250. 101.—Abdomen apex, ♂, ventral, JRJ_01250. 102.—Abdomen apex, ♀, ventral, JRJ_01038. 103.—Interdens, ♀, left lateral, JRJ_01007.

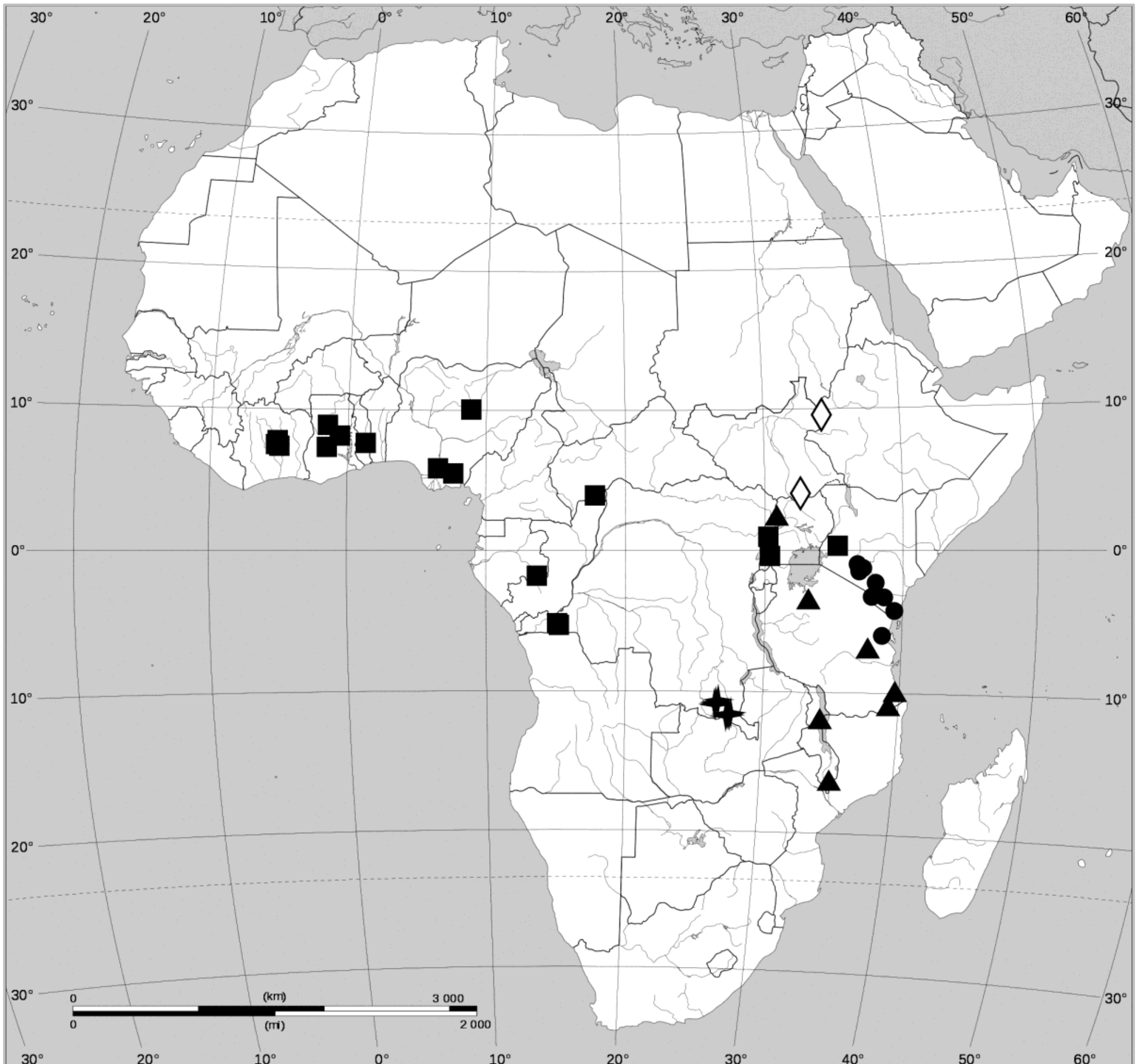


Fig. 104.—Distribution map of *Tmesibasis*: *T. alberti* [+]; *T. imperatrix* [●]; *T. scopsi* [▲]; *T. simplex* [◊]; *T. waelbroecki* [■].

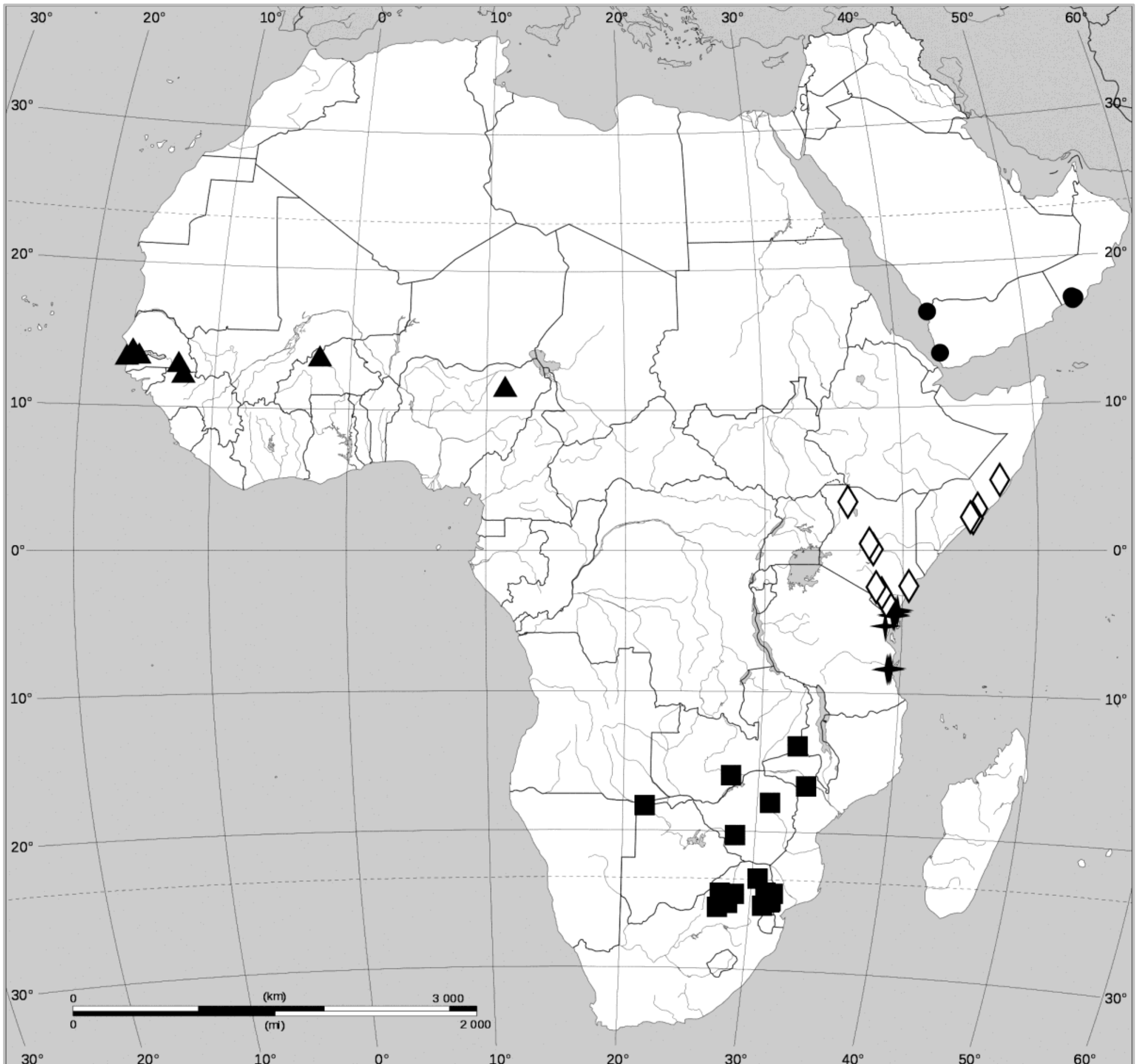


Fig. 105.—Distribution map of *Tmesibasis*: *T. lacerata* [■]; *T. larseni* [●]; *T. majesta* [✚]; *T. rothschildi* [◊]; *T. royi* [▲].

Table 1. ***Tmesibasis*** **cladistic character data matrix.** This table presents cladistic codings of 39 characters for two outgroup and ten ingroup taxa. Data in parentheses (0 1) represent polymorphisms. Question marks (?) represent character states that were unobtainable or uncertain (i.e., missing). See 'Cladistic analysis' for discussion.

	character number																																						
taxon	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**
Allocormodes nigristigma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melambrotus simia	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1
Tmesibasis alberti	1	1	1	1	1	1	1	1	1	2	0	1	1	1	0	0	1	2	1	2	1	1	1	4	1	3	0	2	2	3	0	0	2	1	1	1	0	4	2
Tmesibasis imperatrix	1	1	2	1	1	1	0	1	1	1	1	1	1	1	0	0	1	2	1	2	0	1	1	2	1	1	0	0	3	4	0	0	2	1	1	1	0	4	2
Tmesibasis lacerata	1	1	1	1	1	1	1	1	1	2	0	1	1	1	0	0	1	2	1	2	0	1	1	5	1	1	0	2	3	3	0	0	2	1	1	1	0	4	2
Tmesibasis larseni	1	0	0	0	1	0	0	0	0	2	1	0	1	1	0	1	1	1	1	2	0	1	1	1	0	2	1	1	1	1	0	0	1	1	1	0	0	?	?
Tmesibasis majesta	1	0	2	1	2	1	1	1	1	1	0	1	1	1	0	0	1	2	1	2	0	1	2	2	1	1	0	0	3	4	0	0	2	1	1	1	0	4	4
Tmesibasis rothschildi	1	0	0	0	1	0	0	0	0	2	1	0	1	1	0	1	1	1	1	2	0	1	1	1	0	2	1	1	1	1	0	0	2	1	1	0	0	2	2
Tmesibasis royi	1	1	1	1	1	1	0	1	1	2	0	1	1	1	0	0	1	2	1	2	0	1	1	3	1	1	0	2	2	4	1	1	2	1	1	1	1	3	2
Tmesibasis scopsi	1	1	?	1	1	(0 1)	0	1	1	2	?	1	1	1	0	0	1	2	1	2	0	2	1	3	1	1	0	2	?	?	0	0	2	1	1	1	0	?	?
Tmesibasis simplex	1	1	?	1	1	0	0	1	1	2	?	1	1	1	1	0	1	2	1	2	0	1	1	3	1	1	0	1	?	?	1	0	2	1	1	1	(0 1)	?	?
Tmesibasis waelbroecki	1	1	0	1	1	0	0	1	1	2	0	1	1	1	0	1	1	2	1	2	0	1	1	6	1	1	0	1	2	2	0	0	2	1	1	0	0	4	3

Table 2. List of unambiguous apomorphies, by branch. Syn- and autapomorphies obtained in the cladistic analysis, as optimized by PAUP* onto the final topology (A2 Fig. 1). Consistency index value is given in square brackets following each character change. Ambiguous changes are not reported.

branch	# changes	apomorphic character change(s)
node 0 → node 1	0	no unambiguous apomorphic character changes
node 1 → node 2	8	char. 1: 0→1 [1.000]; char. 10: 0→2 [1.000]; char. 14: 0→1 [1.000]; char. 17: 0→1 [1.000]; char. 19: 0→1 [1.000]; char. 22: 0→1 [1.000]; char. 23: 0→1 [1.000]; char. 28: 0→1 [0.667]
node 2 → node 3	2	char. 11: 0→1 [0.500]; char. 27: 0→1 [1.000]
node 3 → Tmesibasis larseni	0	no unambiguous apomorphic character changes
node 3 → Tmesibasis rothschildi	0	no unambiguous apomorphic character changes
node 2 → node 4	7	char. 2: 0→1 [0.500]; char. 4: 0→1 [1.000]; char. 8: 0→1 [1.000]; char. 9: 0→1 [1.000]; char. 12: 0→1 [1.000]; char. 18: 1→2 [1.000]; char. 25: 0→1 [1.000]
node 4 → Tmesibasis waelbroecki	1	char. 39: 2→3 [1.000]
node 4 → node 5	1	char. 36: 0→1 [1.000]
node 5 → Tmesibasis simplex	2	char. 15: 0→1 [1.000]; char. 31: 0→1 [0.500]
node 5 → node 6	2	char. 6: 0→1 [1.000]; char. 28: 1→2 [0.667]
node 6 → Tmesibasis alberti	4	char. 7: 0→1 [0.333]; char. 21: 0→1 [1.000]; char. 24: 3→4 [1.000]; char. 26: 1→3 [1.000]
node 6 → node 7	5	char. 3: 1→2 [1.000]; char. 10: 2→1 [1.000]; char. 24: 3→2 [1.000]; char. 28: 2→0 [0.667]; char. 29: 2→3 [0.750]
node 6 → Tmesibasis lacerata	3	char. 7: 0→1 [0.333]; char. 24: 3→5 [1.000]; char. 29: 2→3 [0.750]
node 6 → Tmesibasis royi	4	char. 31: 0→1 [0.500]; char. 32: 0→1 [1.000]; char. 37: 0→1 [1.000]; char. 38: 4→3 [1.000]
node 6 → Tmesibasis scopsi	1	char. 22: 1→2 [1.000]
node 7 → Tmesibasis imperatrix	1	char. 11: 0→1 [0.500]
node 7 → Tmesibasis majesta	5	char. 2: 1→0 [0.500]; char. 5: 1→2 [1.000]; char. 7: 0→1 [0.333]; char. 23: 1→2 [1.000]; 39: 2→4 [1.000]

Table 3. List of character state changes, by character. Character states transformations as optimized by PAUP* on the topology obtained in the cladistic analysis (A2 Fig. 1) are presented here. Optimizations are provided in the format [node#: ancestral state→derived state node# <u>OR</u> node#: ancestral state→state of terminal taxon]. Node numbers correspond to those found on A2 Fig. 1. Both unambiguous (→) and ambiguous (-->>) character state changes are provided.

char#	CI	steps	state transformation(s)
1	1.000	1	node 1: 0 → 1 node 2
2	0.500	2	node 2: 0 → 1 node 4; node 7: 1 → 0 Tmesibasis majesta
3	1.000	2	node 4: 0 -->> 1 node 5; node 6: 1 → 2 node 7
4	1.000	1	node 2: 0 → 1 node 4
5	1.000	2	node 0: 0 -->> 1 node 1; node 7: 1 → 2 Tmesibasis majesta
6	1.000	1	node 5: 0 → 1 node 6
7	0.333	3	node 6: 0 → 1 Tmesibasis alberti; node 7: 0 → 1 Tmesibasis majesta; node 6: 0 → 1 Tmesibasis lacerata
8	1.000	1	node 2: 0 → 1 node 4
9	1.000	1	node 2: 0 → 1 node 4
10	1.000	2	node 1: 0 → 2 node 2; node 6: 2 → 1 node 7
11	0.500	2	node 7: 0 → 1 Tmesibasis imperatrix; node 2: 0 → 1 node 3
12	1.000	1	node 2: 0 → 1 node 4
13	1.000	1	node 0: 0 -->> 1 node 1
14	1.000	1	node 1: 0 → 1 node 2
15	1.000	1	node 5: 0 → 1 Tmesibasis simplex
16	0.500	2	node 1: 0 -->> 1 node 2; node 4: 1 -->> 0 node 5
17	1.000	1	node 1: 0 → 1 node 2
18	1.000	2	node 0: 0 -->> 1 node 1; node 2: 1 → 2 node 4
19	1.000	1	node 1: 0 → 1 node 2
20	1.000	2	node 0: 0 -->> 1 node 1; node 1: 1 -->> 2 node 2
21	1.000	1	node 6: 0 → 1 Tmesibasis alberti
22	1.000	2	node 1: 0 → 1 node 2; node 6: 1 → 2 Tmesibasis scopsi
23	1.000	2	node 1: 0 → 1 node 2; node 7: 1 → 2 Tmesibasis majesta
24	1.000	6	node 1: 0 -->> 1 node 2; node 2: 1 -->> 3 node 4; node 6: 3 → 4 Tmesibasis alberti; node 6: 3 → 2 node 7; node 6: 3 → 5 Tmesibasis lacerata; node 4: 3 -->> 6 Tmesibasis
25	1.000	1	node 2: 0 → 1 node 4
26	1.000	3	node 1: 0 -->> 1 node 2; node 6: 1 → 3 Tmesibasis alberti; node 2: 1 -->> 2 node 3
27	1.000	1	node 2: 0 → 1 node 3
28	0.667	3	node 1: 0 → 1 node 2; node 5: 1 → 2 node 6; node 6: 2 → 0 node 7
29	0.750	4	node 1: 0 -->> 1 node 2; node 2: 1 -->> 2 node 4; node 6: 2 → 3 node 7; node 6: 2 → 3 Tmesibasis lacerata
30	0.800	5	node 1: 0 -->> 1 node 2; node 2: 1 -->> 2 node 4; node 4: 2 -->> 3 node 5; node 6: 3 -->> 4 node 7; node 6: 3 -->> 4 Tmesibasis royi
31	0.500	2	node 6: 0 → 1 Tmesibasis royi; node 5: 0 → 1 Tmesibasis simplex
32	1.000	1	node 6: 0 → 1 Tmesibasis royi
33	0.667	3	node 0: 0 -->> 1 node 1; node 1: 1 -->> 2 node 2; node 3: 2 -->> 1 Tmesibasis larseni
34	1.000	1	node 0: 0 -->> 1 node 1
35	1.000	1	node 0: 0 -->> 1 node 1

Table 3. List of character state changes, by character, cont.

char#	CI	steps	state transformation(s)
36	1.000	1	node 4: 0 → 1 node 5
37	1.000	1	node 6: 0 → 1 Tmesibasis royi
38	1.000	4	node 0: 0 -->> 1 node 1; node 1: 1 -->> 2 node 2; node 2: 2 -->> 4 node 4; node 6: 4 → 3 Tmesibasis royi
39	1.000	4	node 0: 0 -->> 1 node 1; node 1: 1 -->> 2 node 2; node 7: 2 → 4 Tmesibasis majesta; node 4: 2 → 3 Tmesibasis waelbroecki

APPENDIX 3

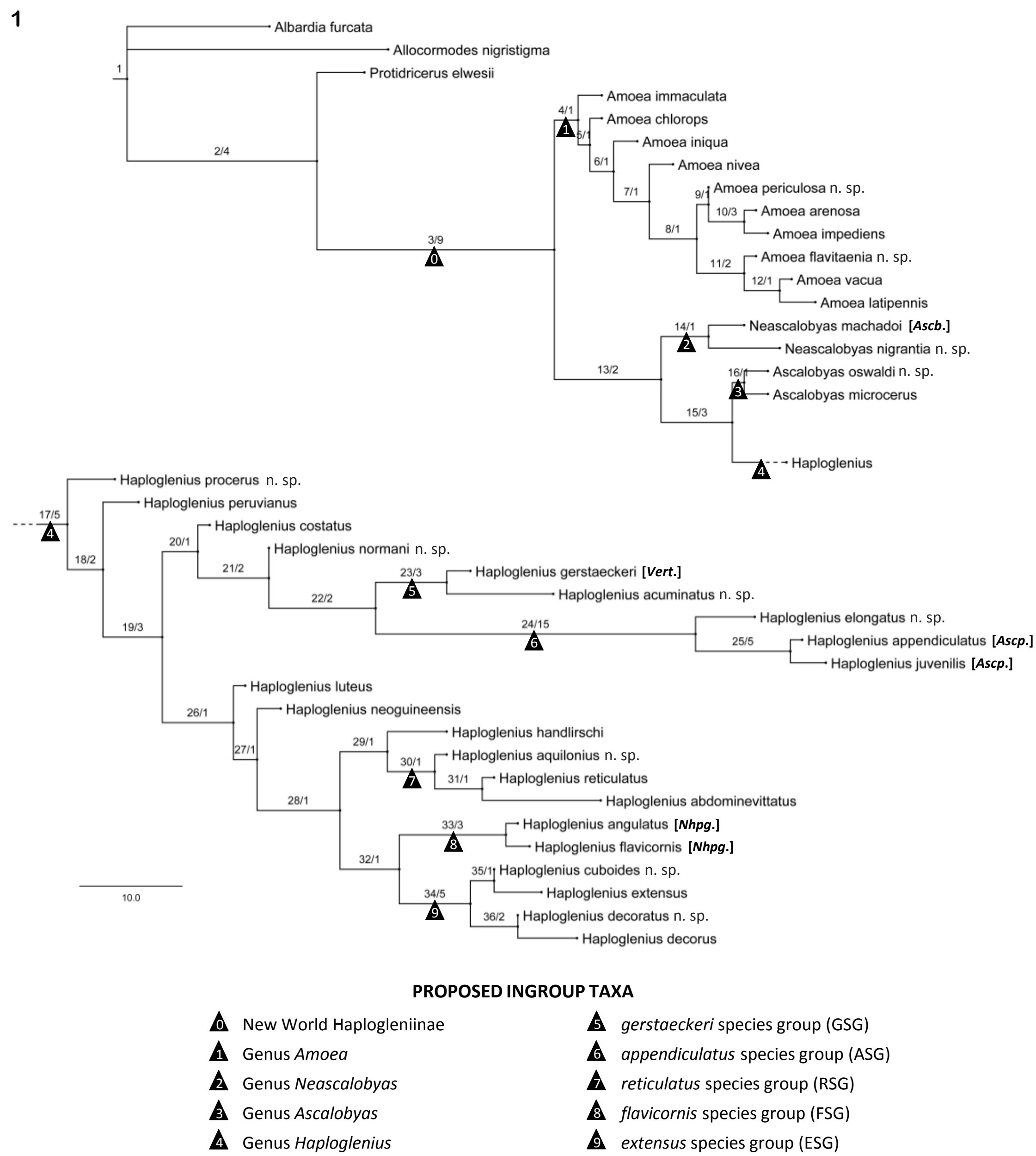
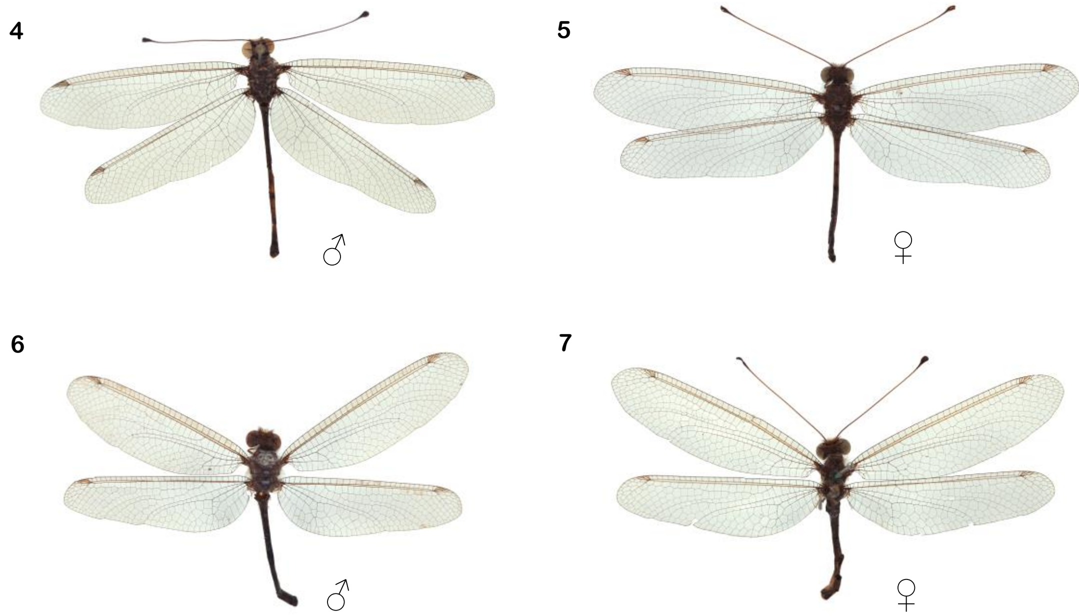


Fig. 1.—Phylogram of New World Haplogleniinae species from TNT and PAUP* analysis of morphological characters, drawn to reflect branch lengths. Outgroup taxa = *Albardia furcata*, *Allocormodes nigristigma*, *Protidricerus elwesii*; # ingroup taxa = 35; # characters = 79; score = 334; C.I. = .6497; R.I. = .7776. Numbers above branches (e.g., 3/9) indicate number of adjacent (downstream) node followed by Bremer support value for that node. Node numbers correspond to the change list (see A3 Table 3; for a list of node synapomorphies and terminal taxon autapomorphies see A3 Table 2 and character list in 'Cladistic analysis'), as well as individual taxon descriptions. Species placed in other genera before this revision are followed by a bracketed abbreviation indicating their previous alliance: [*Ascb.*] = *Ascalobyas* Penny; [*Vert.*] = *Verticillecerus* van der Weele; [*Ascp.*] = *Ascaloptynx* Banks; [*Nhpn.*] = *Neohaploglenius* Penny.

2

3

Figs. 2–3.—*Amoea arenosa* (Walker). 2.—Dorsal habitus, holotype ♂, BMNH, JRJ_01626. 3.—Dorsal habitus, ♀, CMNH, JRJ_00205.



Figs. 4–7.—*Amoea chlorops* (Blanchard). 4.—Dorsal habitus, ♂, UNESP, JRJ_00236. 5.—Dorsal habitus, ♀, BMNH, JRJ_01616. 6.—Dorsal habitus, ♂, MFNB, JRJ_01720. 7.—Dorsal habitus, ♀, MFNB, JRJ_01721.

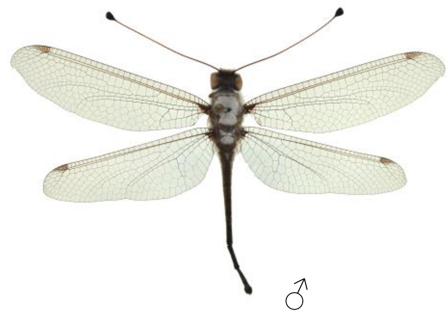
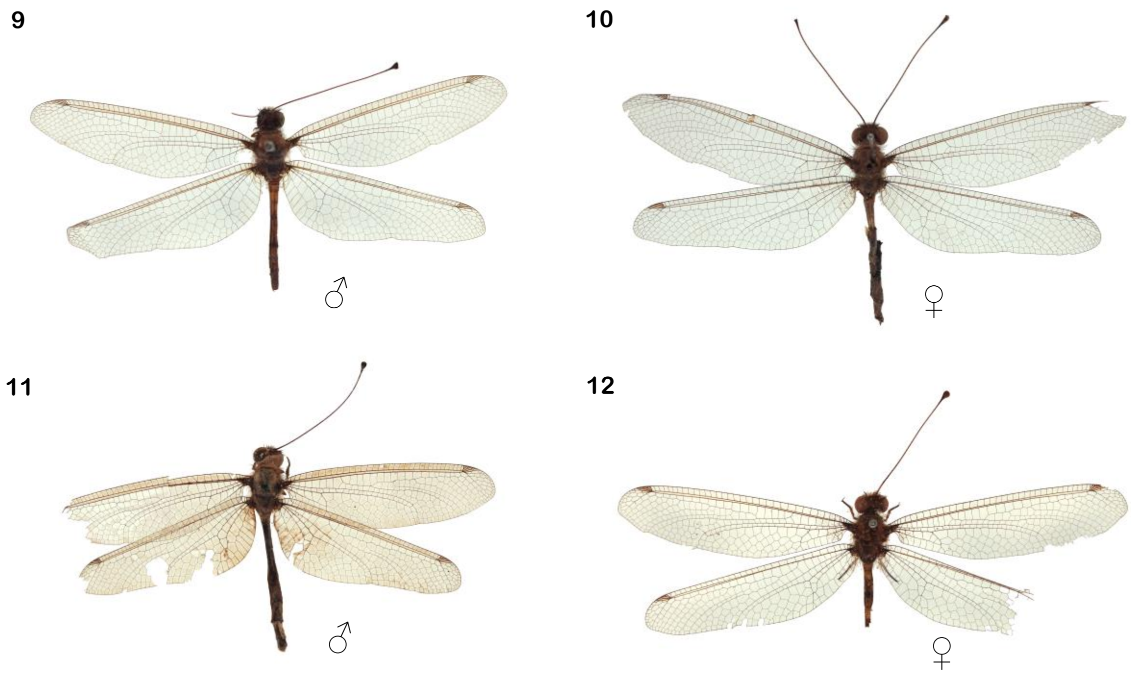


Fig. 8.—*Amoea flavitaenia* n. sp. Dorsal habitus, ♂, CAS, JRJ_00179.



Figs. 9–12.—*Amoea immaculata* (Olivier) and synonyms. 9.—Dorsal habitus, ♂, MFNB, JRJ_01704. 10.—Dorsal habitus, "zaborabas" ♀, MFNB, JRJ_01729. 11.—Dorsal habitus, *Ascalaphus damnosus* Walker holotype ♂, BMNH, JRJ_01613. 12.—Dorsal habitus, *Ascalaphus injurius* Walker holotype ♀, BMNH, JRJ_01625.

13

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Figs. 13–14.—*Amoea impediens* (Walker). 13.—Dorsal habitus, ♂, CMNH, JRJ_00197. 14.—Dorsal habitus, ♀, CMNH, JRJ_00200.

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Figs. 15–16.—*Amoea iniqua* (Walker). 15.—Dorsal habitus, ♂, SDMC, JRJ_00230. 16.—Dorsal habitus, *Ascalaphus iniquus* Walker holotype ♂, BMNH, JRJ_01628.

17

18

Figs. 17–18.—*Amoea latipennis* (Navás). 17.—Dorsal habitus, ♂, CMNH, JRJ_00107. 18.—Dorsal habitus, ♀, UCDC, JRJ_00114.

Fig. 19.—*Amoea nivea* Navás. Dorsal habitus, ♂, CMNH, JRJ_00220.

20

♂

Fig. 20.—*Amoea periculosa* n. sp. Dorsal habitus, ♂, FSCA, JRJ_00191.

21

22

Figs. 21–22.—*Amoea vacua* (Gerstaecker). 21.—Dorsal habitus, ♂, WSU, JRJ_01282. 22.—Dorsal habitus, ♀, NMW, JRJ_00159.

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Figs. 23–24.—*Neascalobyas machadoi* (Penny). 23.—Dorsal habitus, ♂, FSCA, JRJ_00248. 24.—Dorsal habitus, ♀, INPA, JRJ_00257.

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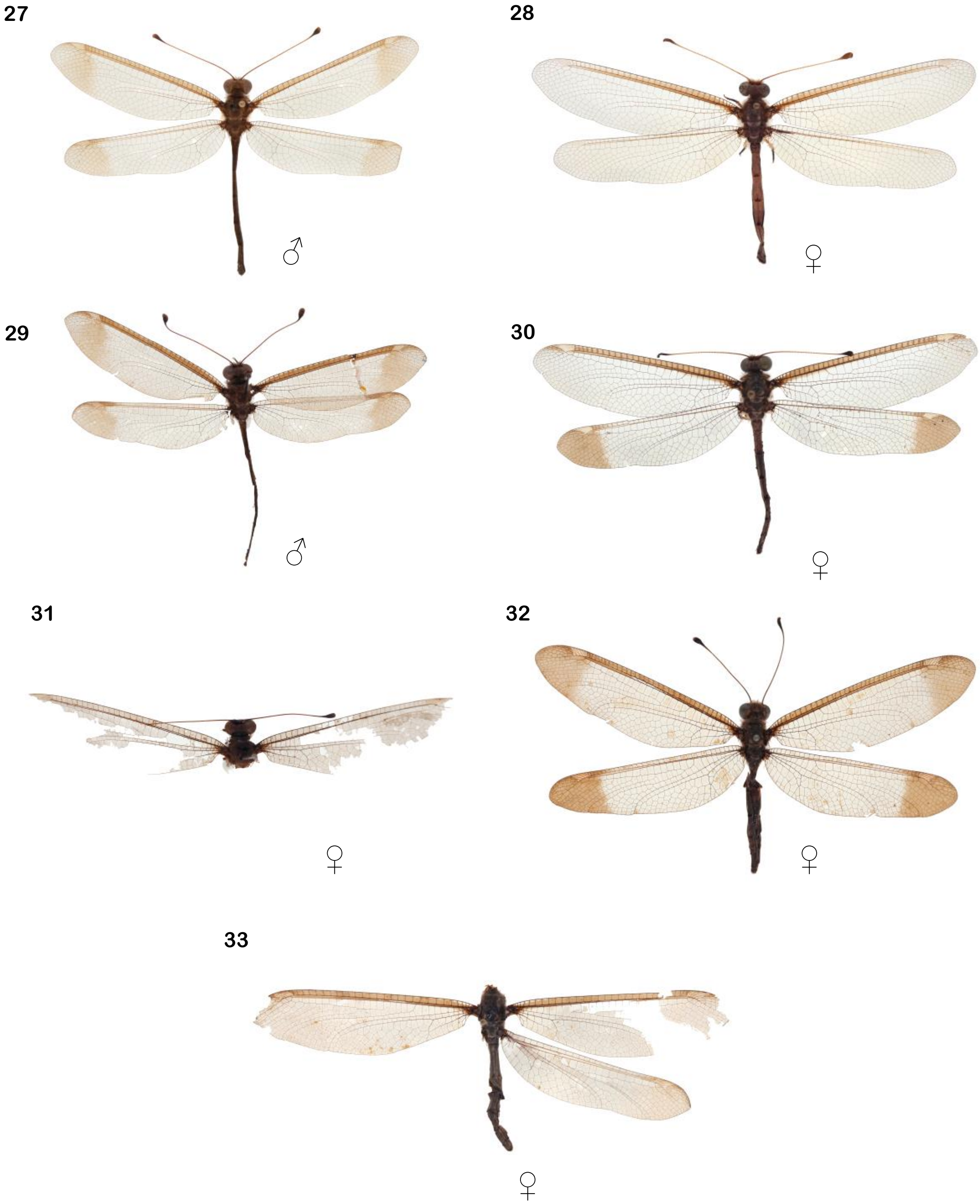
Figs. 25–26.—*Neascalobyas nigrantia* n. sp. 25.—Dorsal habitus, holotype ♂, CAS, JRJ_00269. 26.—Dorsal habitus, ♀, CAS, JRJ_00271.



Figs. 27–33.—*Ascalobyas microcerus* (Rambur) and synonyms. 27.—Dorsal habitus, ♂, CMNH, JRJ_00385. 28.—Dorsal habitus, ♀, FSCA, JRJ_00331. 29.—Dorsal habitus, *Haploglenius camposi* Navás “cotype” (=syntype) ♂, MNHN, JRJ_01223. 30.—Dorsal habitus, ♀, BYU, JRJ_00377. 31.—Dorsal habitus, *Byas microcerus* Rambur holotype ♀, MNHN, JRJ_01217. 32.—Dorsal habitus, ♀, MFNB, JRJ_01849. 33.—Dorsal habitus, *Haploglenius camposi* Navás lectotype ♀, MNHN, JRJ_01221.

34

Fig. 34.—*Ascalobyas oswaldi* n. sp. Dorsal habitus, holotype ♂, INPA, JRJ_00390.

35

36

Figs. 35–36.—*gerstaeckeri* species group: *Haploglenius gerstaeckeri* (van der Weele). 35.—Dorsal habitus, ♂, USNM, JRJ_01040. 36.—Dorsal habitus, ♀, MFNB, JRJ_01041.

37

Fig. 37.—*gerstaeckeri* species group: *Haploglenius acuminatus* n. sp. Dorsal habitus, holotype ♂, INPA, JRJ_01045.

38

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Figs. 38–39.—*appendiculatus* species group: *Haploglenius appendiculatus* (Fabricius). 38.—Dorsal habitus, ♂, JRJC, JRJ_01544. 39.—Dorsal habitus, ♀, FMNH, JRJ_01322.

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Figs. 40–41.—*appendiculatus* species group: *Haploglenius juvenilis* (McLachlan). 40.—Dorsal habitus, ♂, JRJC, JRJ_01513. 41.—Dorsal habitus, ♀, JRJC, JRJ_01532.

42

Fig. 42.—*appendiculatus* species group: *Haploglenius elongatus* n. sp. Dorsal habitus, holotype ♂, FSCA, JRJ_01602.

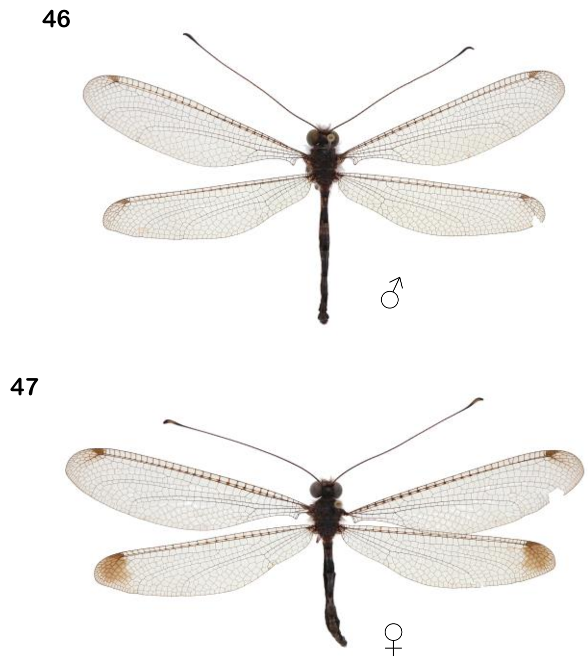
43

44

Figs. 43–44.—*reticulatus* species group: *Haploglenius reticulatus* Navás. 43.—Dorsal habitus, ♂, FSCA, JRJ_00621. 44.—Dorsal habitus, ♀, MFNB, JRJ_00640.

45

Fig. 45.—*reticulatus* species group: *Haploglenius aquilonius* n. sp. Dorsal habitus, holotype ♂, MFNB, JRJ_01754.



Figs. 46–47.—*reticulatus* species group: *Haploglenius abdominevittatus* Ardila and Jones. 46.—Dorsal habitus, ♂, USNM, JRJ_00597. 47.—Dorsal habitus, ♀, USNM, JRJ_00596.

48

Fig. 48.—*flavicornis* species group: *Haploglenius flavicornis* McLachlan. Dorsal habitus, ♀, unknown collection, JRJ_01631.

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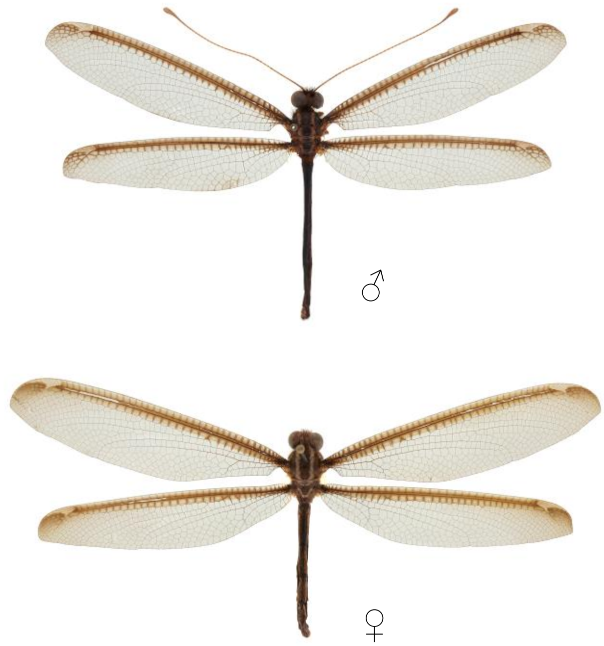
Figs. 49–50.—*flavicornis* species group: *Haploglenius angulatus* Gerstaecker. 49.—Dorsal habitus, ♂, FSCA, JRJ_00772. 50.—Dorsal habitus, ♀, SDMC, JRJ_00879.

51

52



Figs. 51–52.—*extensus* species group: *Haploglenius extensus* Banks. 51.—Dorsal habitus, ♂, FSCA, JRJ_00599. 52.—Dorsal habitus, ♀, FSCA, JRJ_00606.

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54

Figs. 53–54.—*extensus* species group: *Haploglenius cuboides* n. sp. 53.—Dorsal habitus, ♂, TAMU, JRJ_00609. 54.—Dorsal habitus, holotype ♀, FSCA, JRJ_00616.

55

♂

Fig. 55.—*extensus* species group: *Haploglenius decorus* Ábrahám. Dorsal habitus, ♂, MNHN, JRJ_01629.

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57

Figs. 56–57.—*extensus* species group: *Haploglenius decoratus* n. sp. 56.—Dorsal habitus, ♂, BMNH, JRJ_01640. 57.—Dorsal habitus, ♀, MFNB, JRJ_01752.

58

Fig. 58.—unplaced *Haploglenius*: *Haploglenius procerus* n. sp. Dorsal habitus, holotype ♂, CUAC, JRJ_00585.

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Figs. 59–60.—unplaced *Haploglenius*: *Haploglenius peruvianus* van der Weele. 59.—Dorsal habitus, ♂, CAS, JRJ_00623. 60.—Dorsal habitus, ♀, BMNH, JRJ_01636.

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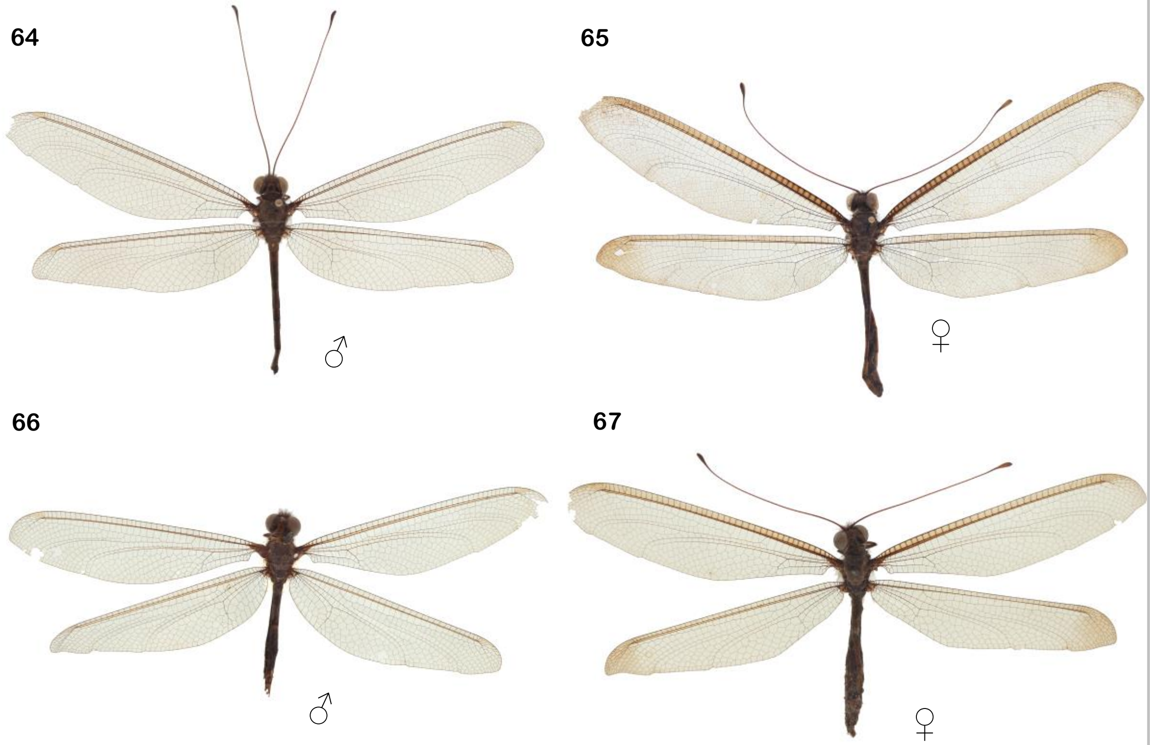
62

Figs. 61–62.—unplaced *Haploglenius*: *Haploglenius costatus* (Burmeister). 61.—Dorsal habitus, ♂, NMW, JRJ_00517. 62.—Dorsal habitus, ♀, NMW, JRJ_00534.

63

♂

Fig. 63.—unplaced *Haploglenius*: *Haploglenius normani* n. sp. Dorsal habitus, ♂, BMNH, JRJ_01643.

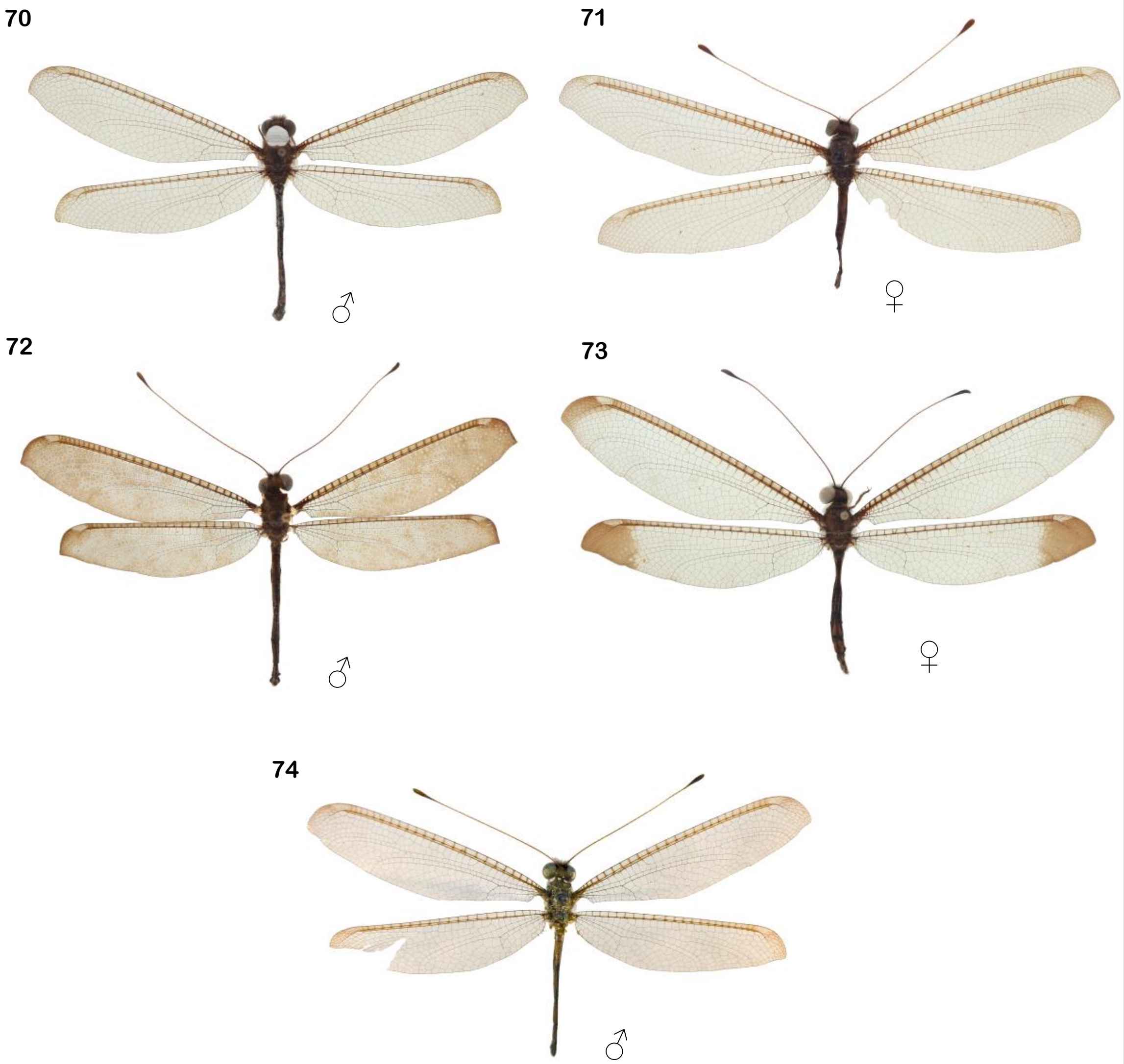


Figs. 64–67.—unplaced *Haploglenius*: *Haploglenius luteus* (Walker) and synonyms. 64.—Dorsal habitus, ♂, INPA, JRJ_00437. 65.—Dorsal habitus, ♀, UCDC, JRJ_00428. 66.—Dorsal habitus, *Ascalaphus luteus* Walker holotype ♂, BMNH, JRJ_01634. 67.—Dorsal habitus, *Ascalaphus circumflexus* Walker holotype ♀, BMNH, JRJ_01635.

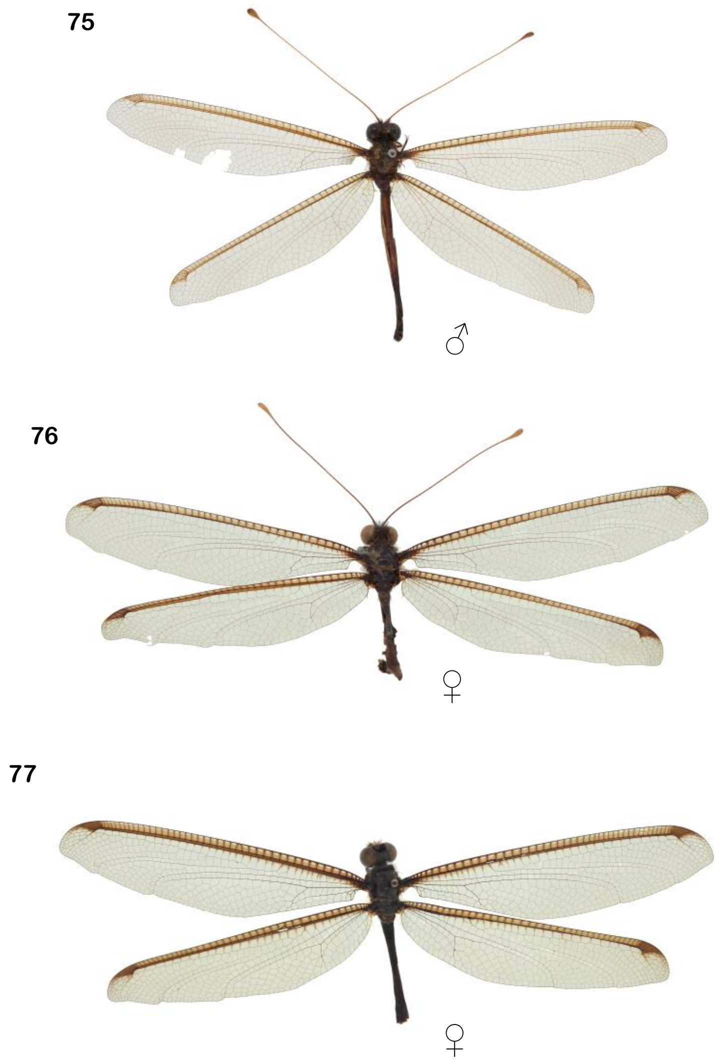
68

69

Figs. 68–69.—unplaced *Haploglenius*: *Haploglenius brunneus* n. sp. 68.—Dorsal habitus, holotype ♂, TAMU, JRJ_00469. 69.—Dorsal habitus, ♀, UCDC, JRJ_00468.



Figs. 70–74.—unplaced *Haploglenius*: *Haploglenius neoguineensis* Navás. 70.—Dorsal habitus, ♂, FSCA, JRJ_00645. 71.—Dorsal habitus, ♀, UMRM, JRJ_00641. 72.—Dorsal habitus, melanistic ♂, MFNB, JRJ_00643. 73.—Dorsal habitus, ♀ with dark wingtips, TAMU, JRJ_00634. 74.—Dorsal habitus, *Haploglenius neoguineensis* Navás holotype ♂, MNCN, JRJ_02000.



Figs. 75–77.—unplaced *Haploglenius*: *Haploglenius handlirschi* van der Weele. 75.—Dorsal habitus, ♂, MFNB, JRJ_01753. 76.—Dorsal habitus, ♀, MFNB, JRJ_01757. 77.—Dorsal habitus, *Haploglenius handlirschi* van der Weele syntype ♀, NMW, JRJ_00582.

78

Fig. 78.—unplaced *Haploglenius*: *Haploglenius legnotos* n. sp. Dorsal habitus, holotype ♀, FSCA, JRJ_00622.

Fig. 79.—Distribution map of *Amoea*: *A. arenosa* [▲]; *A. impediens* [●].

Fig. 80.—Distribution map of *Amoea*: *A. chlorops* [▲]; *A. periculosa* [●].

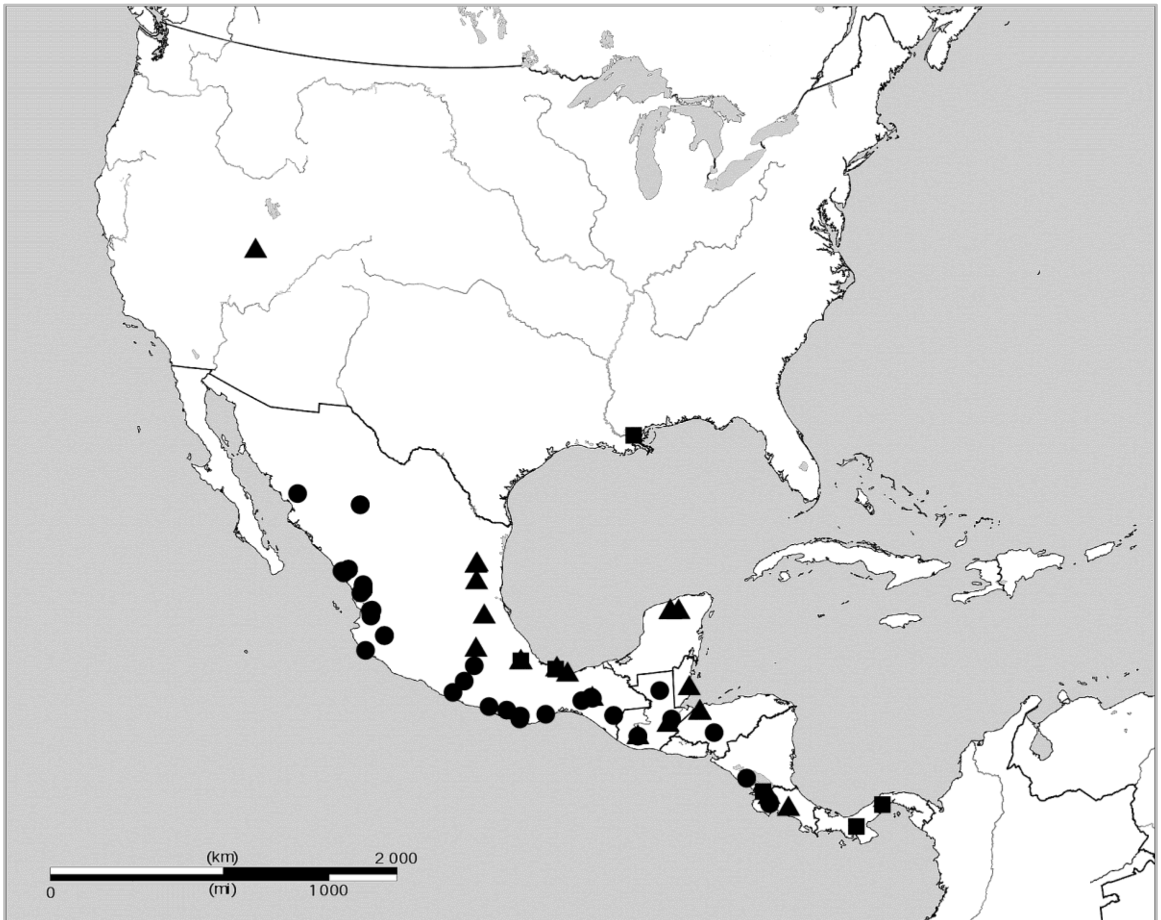


Fig. 81.—Distribution map of *Amoea*: *A. flavitaenia* [■]; *A. latipennis* [●]; *A. vacua* [▲].

Fig. 82.—Distribution map of *Amoea*: *A. immaculata* [■]; *A. iniqua* [▲]; *A. nivea* [●].

Fig. 83.—Distribution map of *Neascalobyas*: *N. machadoi* [●]; *N. nigrantia* [▲].

Fig. 84.—Distribution map of *Ascalobyas*: *A. microcerus* [●]; *A. oswaldi* [▲].

Fig. 85.—Distribution map of *Haploglenius*: *H. gerstaeckeri* [▲]; *H. acuminatus* [●].

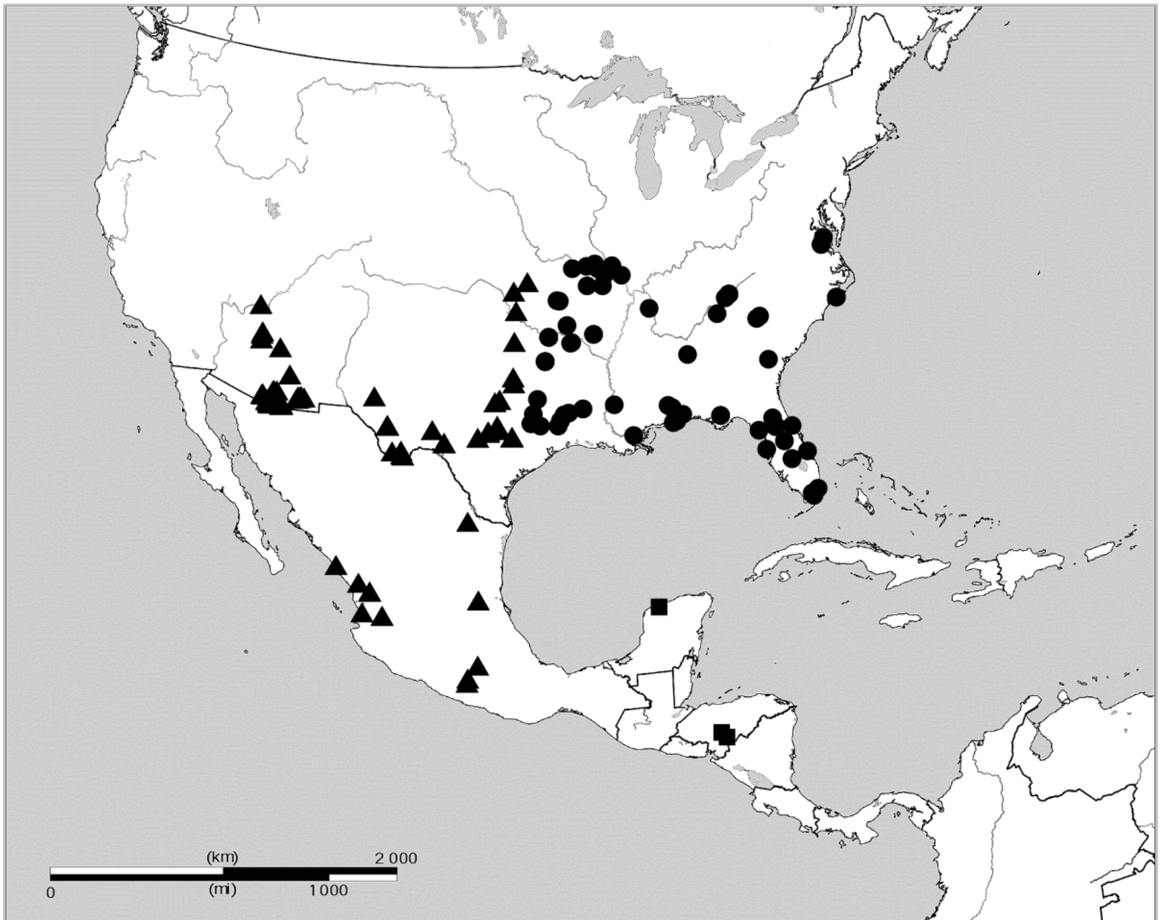


Fig. 86.—Distribution map of *Haploglenius*: *H. appendiculatus* [●]; *H. juvenilis* [▲]; *H. elongata* [■].

Fig. 87.—Distribution map of *Haploglenius*: *H. reticulatus* [▲]; *H. aquilonius* [■]; *H. abdominevittatus* [●].

Fig. 88.—Distribution map of *Haploglenius*: *H. flavicornis* [●].

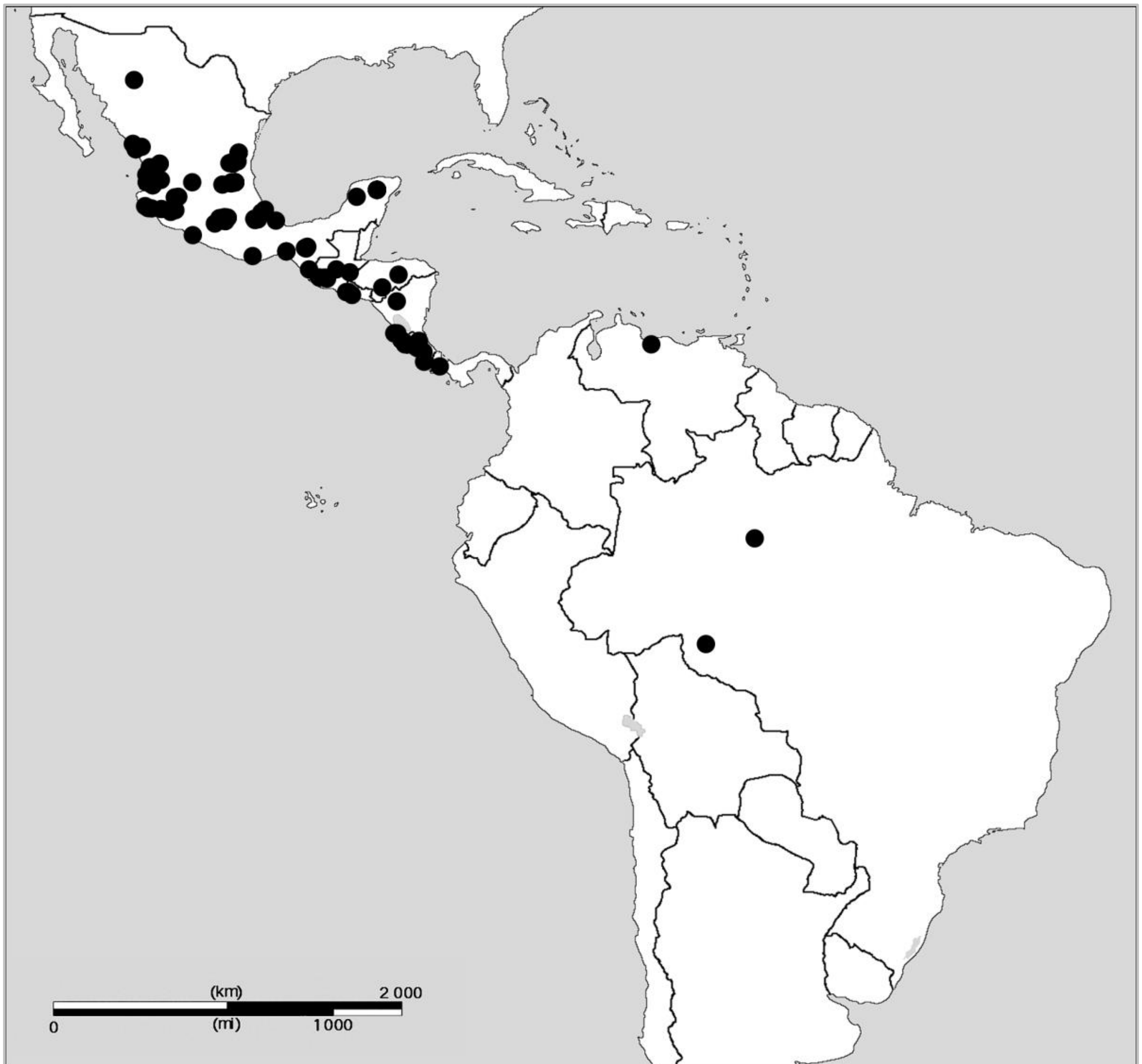


Fig. 89.—Distribution map of *Haploglenius*: *H. angulatus* [●].

Fig. 90.—Distribution map of *Haploglenius*: *H. extensus* [●]; *H. cuboides* [▲]; *H. decorus* [✚]; *H. decoratus* [■].

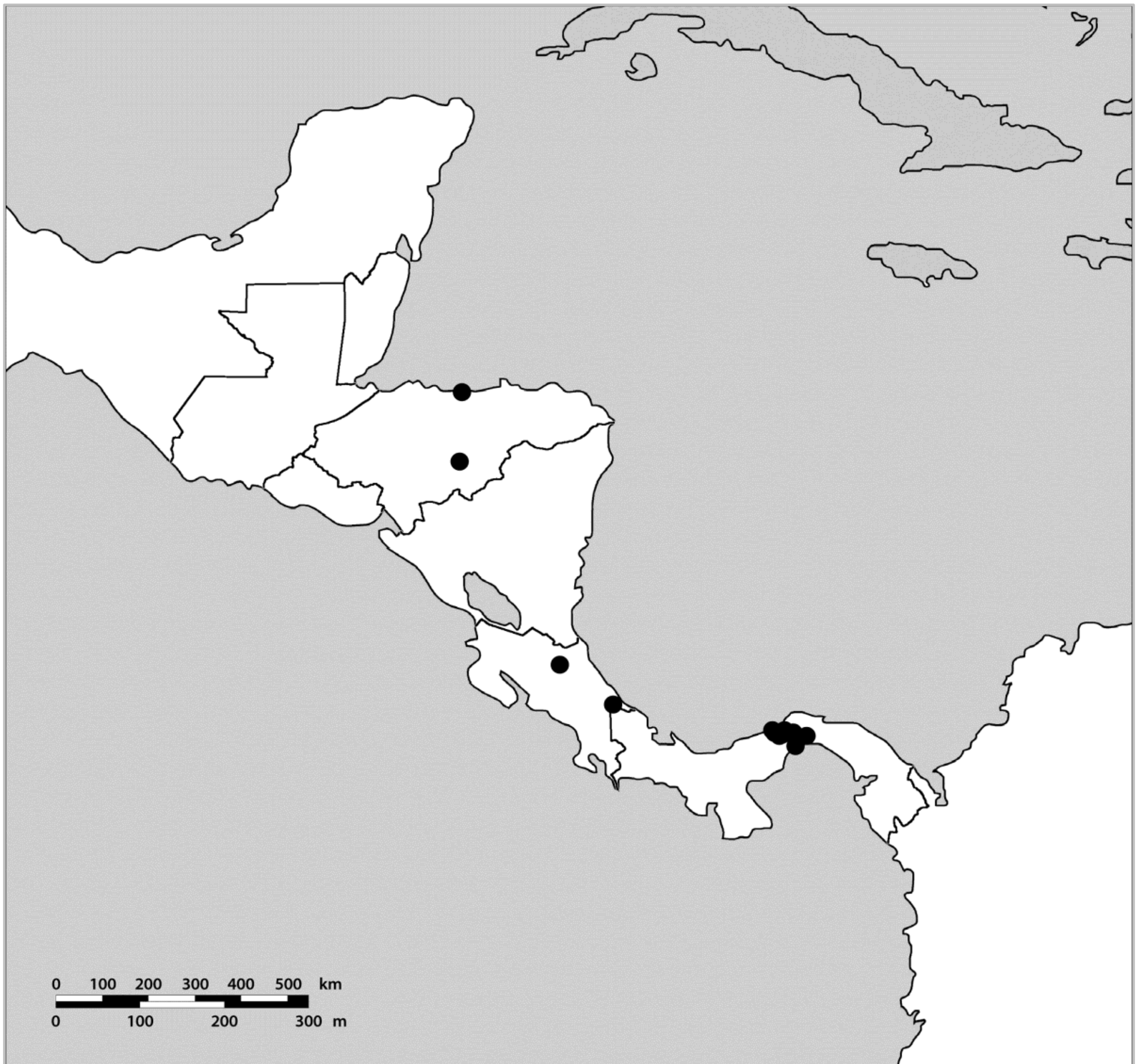


Fig. 91.—Distribution map of *Haploglenius*: *H. procerus* [●].

Fig. 92.—Distribution map of *Haploglenius*: *H. peruvianus* [●]; *H. costatus* [▲].

Fig. 93.—Distribution map of *Haploglenius*: *H. normani* [●]; *H. legnotos* [▲].

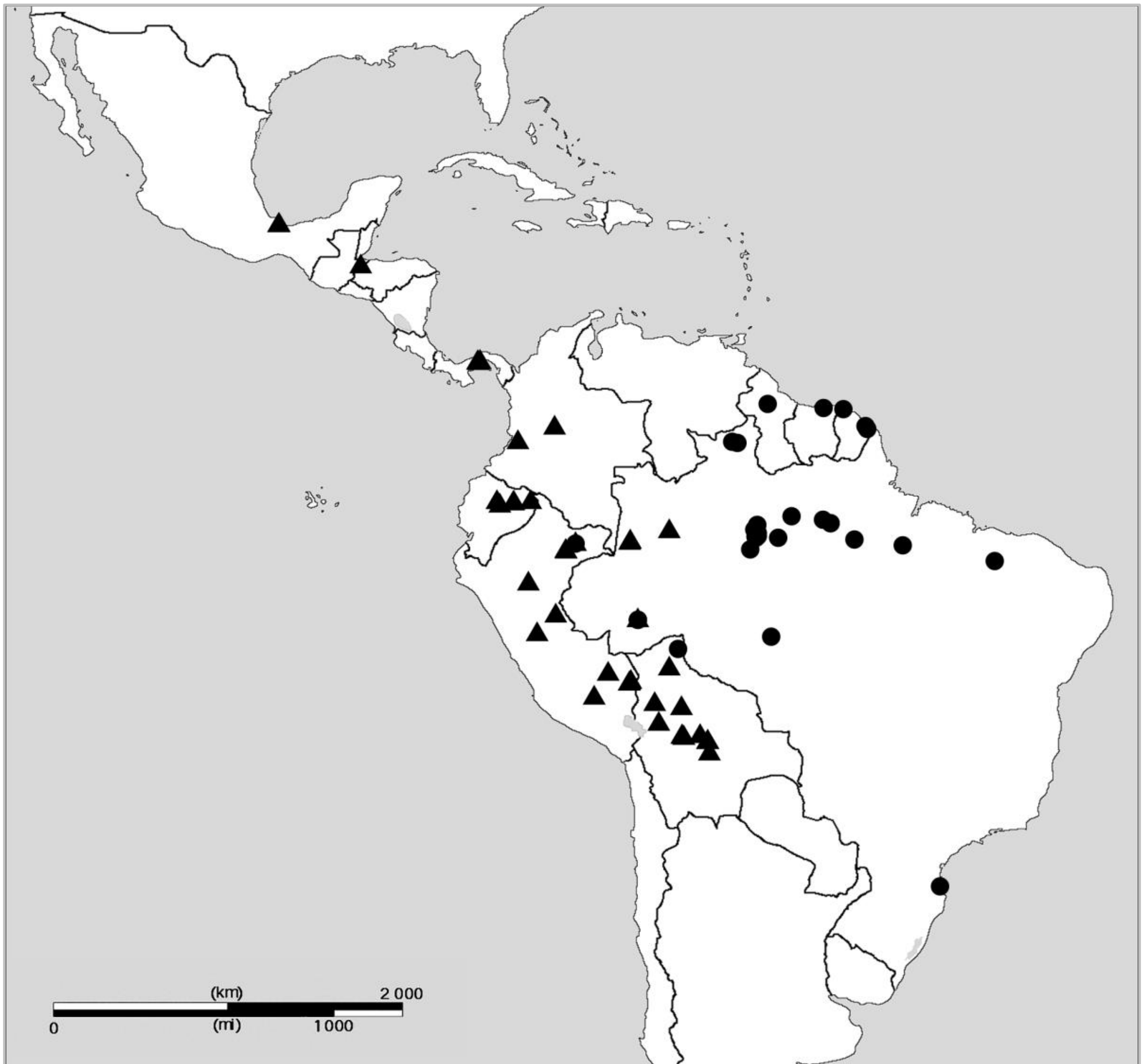


Fig. 94.—Distribution map of *Haploglenius*: *H. luteus* [●]; *H. brunneus* [▲].

Fig. 95.—Distribution map of *Haploglenius*: *H. neoguineensis* [●]; *H. handlirschi* [▲].

Table 1. New World Haplogleniinae cladistic character data matrix. This table presents cladistic codings of 79 characters for three outgroup and 35 ingroup taxa. Data in square brackets [0 1] represent polymorphisms. Question marks (?) represent character states that were unobtainable or uncertain (i.e., missing). One character was coded for more than ten states and states above 9 were coded as letters per requirements in TNT. Numbering of characters is presented as required for analysis in PAUP*, beginning with 1, rather than for TNT, which begins with 0. See 'Cladistic analysis' for discussion.

	character number																										
taxon	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
Albardia furcata	0	0	0	0	0	0	0	1	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	6
Allocormodes nigristigma	[0 1]	0	1	0	0	1	2	1	0	0	1	0	0	2	0	0	1	1	1	0	0	0	0	0	1	1	0
Protidricerus elwesii	0	0	1	1	0	1	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1
Amoea latipennis	1	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	2	0	1	0	[1 6]	0	0	1	3	2	0
Amoea vacua	1	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	2	0	1	0	[1 6]	0	0	1	3	[1 2]	0
Amoea flavitaenia	1	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	2	0	1	0	1	0	0	1	3	2	0
Amoea periculosa	1	1	2	?	2	2	2	0	0	0	0	?	0	?	0	0	?	0	1	0	1	0	0	?	3	2	0
Amoea impediens	1	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	1	0	3	2	0
Amoea arenosa	1	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	0	3	2	0
Amoea nivea	1	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	1	0	1	0	2	0	0	0	3	2	0
Amoea iniqua	1	1	2	0	2	2	2	0	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	3	2	0
Amoea chlorops	1	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	2	0	1	0	3	0	0	0	3	2	0
Amoea immaculata	0	1	2	0	2	2	2	0	0	0	0	0	0	1	0	0	1	[0 1]	1	0	3	0	0	0	3	2	0
Ascalobyas microcerus	0	1	2	0	2	2	1	0	0	0	0	1	1	3	1	0	1	0	[0 1]	[0 1]	3	0	2	0	3	2	0
Ascalobyas oswaldi	0	1	2	0	2	2	1	0	0	5	0	1	1	3	1	0	1	0	0	0	3	0	0	0	3	2	0
Neascalobyas machadoi	1	1	2	0	2	2	1	0	0	0	0	1	1	4	1	0	1	0	[0 1]	0	0	0	0	0	3	1	0
Neascalobyas nigrantia	0	1	2	1	3	2	1	0	0	2	0	1	1	5	0	0	1	0	0	0	0	0	0	0	3	2	0
Haploglenius procerus	0	1	2	0	2	2	1	0	0	1	0	1	0	7	1	0	1	0	0	0	5	0	0	3	3	2	0
Haploglenius peruvianus	[0 1]	1	2	0	1	2	2	0	0	1	0	1	0	7	1	0	1	0	1	0	5	0	0	3	3	2	0
Haploglenius costatus	0	1	2	0	2	2	2	2	0	1	3	1	0	7	1	0	1	0	[0 1]	0	5	0	0	3	3	2	2
Haploglenius normani	1	1	2	0	2	2	2	2	0	1	3	1	0	0	1	0	1	0	1	0	5	0	0	3	3	2	2
Haploglenius acuminatus	1	1	2	?	2	3	2	2	0	1	3	?	0	?	0	0	?	0	1	2	5	0	0	3	4	4	5
Haploglenius gerstaeckeri	1	1	2	0	2	3	2	2	0	[0 1]	3	1	0	A	0	0	1	0	1	2	5	0	0	3	4	4	2
Haploglenius elongatus	[0 1]	1	2	0	1	2	[1 2]	3	1	1	2	1	0	6	0	0	3	3	1	0	4	0	3	2	2	2	3
Haploglenius appendiculatus	0	1	2	0	2	2	1	3	1	3	2	0	0	6	0	0	3	2	1	[0 1]	4	0	3	2	2	1	4
Haploglenius juvenilis	[0 1]	1	2	0	2	2	1	3	1	3	2	0	0	6	0	0	3	2	1	1	4	0	3	2	2	1	4
Haploglenius luteus	0	1	2	0	3	[1 2]	2	0	0	1	3	1	0	B	1	1	1	0	[0 1]	0	5	0	0	3	2	2	1
Haploglenius neoguineensis	0	1	2	0	3	1	2	0	0	1	3	1	0	B	1	1	1	0	1	0	5	0	0	3	2	2	1
Haploglenius handlirschi	0	1	2	0	3	1	2	0	0	1	3	0	0	0	0	0	1	0	1	0	5	0	0	0	2	2	1
Haploglenius aquilonius	0	1	2	0	3	2	2	0	0	4	3	0	0	9	0	0	1	0	1	0	5	0	0	0	2	2	2
Haploglenius reticulatus	0	1	2	0	3	2	2	0	0	4	3	0	0	9	0	0	1	3	1	0	5	0	0	0	2	2	1
Haploglenius abdominevittatus	0	1	2	0	2	2	2	0	0	4	3	1	0	9	1	0	1	3	1	0	6	0	0	0	2	3	3
Haploglenius angulatus	0	1	2	0	2	2	2	0	0	[0 1]	3	0	0	9	0	0	1	3	1	0	5	0	0	3	2	2	3
Haploglenius flavicornis	0	1	2	0	2	2	2	0	0	[0 1]	3	0	0	9	0	0	1	3	1	0	5	0	0	3	2	2	3
Haploglenius extensus	[0 1]	1	2	0	2	2	2	1	0	[0 1]	3	0	0	6	0	0	1	0	1	1	5	0	0	3	3	2	1
Haploglenius cuboides	0	1	2	0	2	2	2	0	0	1	3	0	0	[0 6]	0	0	1	0	1	1	5	0	0	3	3	2	0
Haploglenius decoratus	0	1	2	0	2	2	2	0	0	1	4	0	0	6	0	0	1	0	1	[0 1]	5	0	0	3	3	2	0
Haploglenius decorus	0	1	2	0	2	2	2	0	0	1	4	0	0	0	0	0	1	0	1	0	5	0	0	3	3	2	0

Table 1. New World Haplogleniinae cladistic character data matrix, cont.

	character number																									
taxon	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**
Albardia furcata	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Allocormodes nigristigma	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	2	2	0	0	0	0	2	1	3	0	1	0
Protidricerus elwesii	0	3	0	0	0	0	1	0	1	1	1	0	0	0	1	2	1	0	0	0	0	0	0	1	1	0	1
Amoea latipennis	0	2	0	0	0	0	1	0	1	1	0	2	0	0	0	1	1	0	0	0	1	0	0	1	1	1	1
Amoea vacua	0	2	0	0	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Amoea flavitaenia	0	2	0	0	0	0	1	0	1	1	0	2	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1
Amoea periculosa	0	?	0	0	0	0	1	0	1	1	0	2	0	0	0	2	1	?	0	0	0	0	0	1	1	1	1
Amoea impediens	0	2	0	0	0	0	1	0	1	1	1	2	0	0	0	2	1	0	0	0	0	0	0	1	1	1	1
Amoea arenosa	0	2	0	0	0	0	1	0	1	1	1	2	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Amoea nivea	0	4	0	0	0	0	1	0	1	1	0	2	0	0	0	2	1	0	0	0	0	0	0	1	1	1	1
Amoea iniqua	0	2	0	0	0	0	1	0	[1 2]	1	[0 1]	2	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Amoea chlorops	0	3	0	0	0	0	1	0	1	1	0	2	0	0	0	0	1	[0 1]	0	0	0	0	0	1	1	1	1
Amoea immaculata	0	3	0	0	0	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1
Ascalobyas microcerus	0	3	0	0	0	0	1	0	[1 2]	1	0	2	0	0	0	5	1	1	0	0	0	1	0	1	1	1	2
Ascalobyas oswaldi	0	3	0	0	0	0	1	0	[1 2]	1	0	2	0	0	0	4	1	1	0	0	0	1	0	1	1	1	[1 2]
Neascalobyas machadoi	0	3	1	1	0	0	1	0	1	1	1	2	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Neascalobyas nigrantia	0	3	1	1	0	0	1	0	1	1	0	2	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1
Haploglenius procerus	0	0	0	0	0	0	2	1	2	1	0	3	0	0	0	5	2	1	0	0	0	1	0	1	1	1	2
Haploglenius peruvianus	0	1	0	0	0	0	1	1	2	1	0	3	0	0	0	5	1	1	0	0	0	1	0	1	1	1	2
Haploglenius costatus	0	0	0	0	0	0	1	1	2	1	0	3	0	0	0	5	1	1	0	0	0	1	0	1	1	1	1
Haploglenius normani	0	1	0	0	0	0	1	2	[1 2]	1	0	3	0	0	0	4	1	1	0	0	0	1	0	1	1	1	1
Haploglenius acuminatus	1	7	0	0	0	0	1	3	3	1	0	3	0	0	2	5	?	?	0	1	0	1	2	3	0	1	0
Haploglenius gerstaeckeri	1	6	0	0	0	0	1	2	1	1	0	3	0	0	0	4	0	1	0	0	0	1	0	1	1	1	1
Haploglenius elongatus	1	7	0	0	0	0	1	2	3	1	1	3	0	0	0	4	0	0	0	0	0	0	0	2	1	2	1
Haploglenius appendiculatus	1	7	0	0	2	0	1	2	3	1	1	3	0	0	0	4	0	1	0	0	0	0	0	2	1	2	1
Haploglenius juvenilis	1	7	0	0	2	0	1	2	3	1	1	3	0	0	0	4	0	1	0	0	0	0	0	2	1	2	1
Haploglenius luteus	0	0	0	0	1	0	[1 2]	1	2	1	0	3	0	0	0	4	1	1	[0 1]	0	0	1	0	1	1	1	1
Haploglenius neoguineensis	0	0	0	0	[0 1]	0	1	1	2	1	0	3	0	0	0	4	1	1	1	0	0	1	0	1	1	1	1
Haploglenius handlirschi	0	1	0	0	[0 1]	0	2	1	2	1	0	3	0	0	0	5	1	1	0	0	0	1	0	1	2	[1 3]	1
Haploglenius aquilonius	0	1	0	0	0	0	2	1	2	1	0	3	0	0	0	4	1	1	1	0	0	1	0	1	1	1	1
Haploglenius reticulatus	0	0	0	0	0	0	2	1	2	1	0	3	0	0	0	4	1	1	1	0	0	0	0	1	1	1	1
Haploglenius abdominevittatus	0	5	0	0	0	1	1	1	2	1	0	3	0	0	0	4	0	1	1	0	0	0	0	1	1	1	1
Haploglenius angulatus	1	5	0	0	0	0	1	0	1	1	0	3	0	0	0	2	[0 1]	1	0	0	0	1	0	2	1	1	1
Haploglenius flavicornis	1	6	0	0	0	0	1	1	1	1	0	3	0	0	0	4	0	1	0	0	0	1	0	2	1	1	1
Haploglenius extensus	0	5	0	0	0	0	[1 2]	0	[1 2]	1	0	3	0	0	0	5	1	1	0	0	0	1	2	1	1	3	3
Haploglenius cuboides	0	0	0	0	0	0	2	0	2	1	0	3	0	0	0	5	1	1	0	0	0	1	0	1	1	3	3
Haploglenius decoratus	0	0	0	0	0	0	2	0	2	1	0	4	1	0	0	5	1	1	0	0	0	1	3	1	1	1	3
Haploglenius decorus	0	0	0	0	0	0	2	0	2	1	0	5	1	1	0	5	1	1	1	0	0	1	3	1	1	1	3

Table 1. New World Haplogleniinae cladistic character data matrix, cont.

	character number																								
taxon	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**
Albardia furcata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allocormodes nigristigma	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	2	0	1	1	1
Protidricerus elwesii	0	0	0	0	0	1	2	2	0	0	0	0	0	0	0	0	2	0	2	2	2	1	2	1	2
Amoea latipennis	0	0	2	0	1	2	6	6	0	0	0	0	0	0	0	0	2	0	2	3	2	4	3	2	2
Amoea vacua	0	0	1	0	1	2	6	6	0	0	0	0	0	0	0	0	2	1	2	3	2	4	3	2	2
Amoea flavitaenia	0	0	1	0	1	3	6	5	0	0	0	0	2	0	0	0	2	1	2	3	2	2	3	2	2
Amoea periculosa	0	0	1	0	?	3	?	?	0	0	0	0	?	0	0	0	?	?	?	?	?	3	3	2	2
Amoea impediens	0	0	1	0	1	2	[3 5]	6	0	0	0	0	2	0	0	0	2	1	2	3	2	3	?	?	?
Amoea arenosa	0	0	1	0	1	2	5	6	0	0	0	0	2	0	0	0	2	1	2	3	2	3	3	2	2
Amoea nivea	0	0	1	0	1	4	4	4	0	0	0	0	0	0	0	0	2	1	2	3	2	?	?	?	?
Amoea iniqua	0	0	1	0	1	3	3	3	0	0	0	0	0	0	0	0	2	1	2	3	1	2	3	2	2
Amoea chlorops	0	0	1	0	1	3	3	3	0	0	0	0	0	0	0	0	?	?	?	?	?	2	3	2	2
Amoea immaculata	0	0	1	0	1	3	3	3	0	0	0	0	2	0	0	0	?	?	?	?	?	2	?	?	?
Ascalobyas microcerus	1	1	3	0	1	3	3	3	0	0	0	0	[0 2]	0	0	0	3	1	2	4	2	[2 5]	2	2	2
Ascalobyas oswaldi	1	?	3	0	1	3	3	3	0	0	0	0	0	0	0	0	3	1	2	5	2	?	?	?	?
Neascalobyas machadoi	0	0	3	0	1	3	3	3	0	0	0	0	0	0	0	0	3	1	2	5	2	5	2	2	2
Neascalobyas nigrantia	0	0	3	0	1	3	3	3	0	0	0	0	0	0	0	0	3	1	2	5	1	5	2	2	2
Haploglenius procerus	0	0	3	0	1	3	3	3	0	0	0	0	0	0	0	0	3	1	2	5	1	2	2	2	2
Haploglenius peruvianus	0	1	3	0	1	3	3	3	0	0	0	0	0	0	1	1	3	1	2	5	1	5	2	2	2
Haploglenius costatus	0	1	3	0	1	3	3	3	0	0	0	0	1	0	1	0	3	1	2	5	1	0	2	2	2
Haploglenius normani	0	1	3	0	1	3	3	3	0	0	0	0	1	0	0	0	3	1	2	5	3	[0 5]	2	2	2
Haploglenius acuminatus	0	0	3	0	?	6	?	?	0	?	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?
Haploglenius gerstaeckeri	0	0	3	0	1	6	3	3	0	0	0	0	1	0	0	0	3	1	2	5	3	0	2	2	2
Haploglenius elongatus	0	0	6	0	2	5	7	7	0	0	0	0	2	2	0	0	1	0	3	6	5	7	?	?	?
Haploglenius appendiculatus	0	0	5	1	1	5	7	7	1	0	0	0	2	2	0	0	1	0	3	6	5	7	2	2	0
Haploglenius juvenilis	0	0	4	1	1	5	6	7	2	0	0	0	2	2	0	0	1	0	3	6	5	6	2	2	0
Haploglenius luteus	0	1	3	0	1	3	3	3	0	0	0	0	1	0	3	3	3	1	2	5	1	5	2	2	2
Haploglenius neoguineensis	0	1	3	0	1	3	3	3	0	1	0	0	1	0	3	3	3	1	2	5	1	5	3	2	2
Haploglenius handlirschi	0	1	3	0	1	3	3	3	0	1	0	0	1	0	1	1	3	1	2	5	4	0	3	2	2
Haploglenius aquilonius	0	1	3	0	1	3	3	3	0	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?
Haploglenius reticulatus	0	?	3	0	1	3	3	3	0	0	0	0	1	0	2	2	3	1	2	5	4	?	?	?	?
Haploglenius abdominevittatus	0	0	3	0	1	3	3	3	0	0	0	0	1	0	1	?	?	?	?	?	?	8	?	?	?
Haploglenius angulatus	0	1	3	0	1	3	3	3	0	1	1	[1 2]	1	0	3	2	3	1	2	5	4	[0 5]	3	2	2
Haploglenius flavicornis	0	1	3	0	1	3	3	3	0	1	1	2	1	0	3	2	3	1	2	5	4	[0 5]	3	2	2
Haploglenius extensus	0	0	3	0	1	3	3	3	0	1	1	1	1	0	2	2	3	1	2	5	4	5	3	2	2
Haploglenius cuboides	0	0	3	0	1	3	3	3	0	1	1	1	1	0	2	2	3	1	2	5	4	5	3	2	2
Haploglenius decoratus	0	0	3	0	1	3	3	3	0	1	1	1	1	0	2	2	3	1	2	5	4	?	?	?	?
Haploglenius decorus	0	0	3	0	1	3	3	3	0	1	1	1	1	0	3	2	3	1	2	5	4	?	?	?	?

Table 2. List of unambiguous apomorphies, by branch. Syn- and autapomorphies obtained in the cladistic analysis, as optimized by PAUP* onto the final topology (A3 Fig. 1), are presented here. Consistency index value is given in square brackets following each character change. Ambiguous

branch	# changes	apomorphic character change(s)
node_1 → Albardia furcata	11	char. 3: 1 →0 [1.000]; char. 6: 1→0 [0.600]; char. 7: 2→0 [0.500]; char. 17: 1→0 [0.750]; char. 27: 0→6 [0.500]; char. 36: 1→0 [0.600]; char. 38: 0→2 [0.400]; char. 43: 2→3 [0.357]; char. 60: 1→0 [0.857]; char. 75: 2→0 [0.714]; char. 78: 1→0 [1.000]
node_1 → Allocormodes nigristigma	10	char. 11: 0→1 [1.000]; char. 18: 0→1 [0.600]; char. 19: 0→1 [0.333]; char. 26: 0→1 [0.667]; char. 30: 0→1 [0.500]; char. 37: 1→0 [1.000]; char. 39: 0→1 [1.000]; char. 49: 0→2 [0.500]; char. 50: 0→1 [0.750]; char. 68: 0→1 [1.000]
node_1 → node_2	5	char. 8: 1→0 [0.750]; char. 29: 0→3 [0.500]; char. 34: 0→1 [0.400]; char. 52: 0→1 [0.667]; char. 54: 0→1 [0.600]
node_2 → Protidricerus elwesii	4	char. 4: 0→1 [0.500]; char. 27: 0→1 [0.500]; char. 38: 0→1 [0.400]; char. 42: 0→1 [1.000]
node_2 → node_3	11	char. 2: 0→1 [1.000]; char. 3: 1→2 [1.000]; char. 5: 0→2 [0.429]; char. 6: 1→2 [0.600]; char. 26: 0→2 [0.667]; char. 39: 0→2 [1.000]; char. 43: 2→0 [0.357]; char. 59: 0→1 [1.000]; char. 60: 1→3 [0.857]; char. 72: 0→1 [0.333]; char. 78: 1→2 [1.000]
node_3 → node_4	1	char. 19: 0→1 [0.333]
node_4 → node_5	1	char. 1: 0→1 [0.250]
node_5 → node_6	2	char. 21: 3→2 [0.857]; char. 29: 3→2 [0.500]
node_6 → node_7	1	char. 43: 0→2 [0.357]
node_7 → node_8	1	char. 21: 2→1 [0.857]
node_8 → node_11	3	char. 17: 1→2 [0.750]; char. 24: 0→1 [0.750]; char. 43: 2→1 [0.357]
node_11 → node_12	2	char. 60: 3→2 [0.857]; char. 76: 2→4 [0.727]
node_12 → Amoea latipennis	3	char. 48: 0→1 [1.000]; char. 57: 1→2 [1.000]; char. 72: 1→0 [0.333]
node_12 → Amoea vacua	1	char. 43: 1→0 [0.357]
node_11 → Amoea flavitaenia	1	char. 62: 6→5 [1.000]
node_8 → node_9	1	char. 76: 2→3 [0.727]
node_9 → node_10	3	char. 20: 0→1 [0.500]; char. 38: 0→1 [0.400]; char. 60: 3→2 [0.857]
node_10 → Amoea impediens	2	char. 22: 0→1 [1.000]; char. 23: 0→1 [1.000]
node_10 → Amoea arenosa	1	char. 43: 2→0 [0.357]
node_7 → Amoea nivea	2	char. 29: 2→4 [0.500]; char. 60: 3→4 [0.857]
node_6 → Amoea iniqua	2	char. 14: 1→0 [0.688]; char. 75: 2→1 [0.714]
node_5 → Amoea chlorops	1	char. 17: 1→2 [0.750]
node_4 → Amoea immaculata	2	char. 45: 0→1 [0.333]; char. 67: 0→2 [0.400]
node_3 → node_13	3	char. 7: 2→1 [0.500]; char. 12: 0→1 [0.250]; char. 71: 2→3 [0.750]
node_13 → node_15	4	char. 43: 0→5 [0.357]; char. 45: 0→1 [0.333]; char. 49: 0→1 [0.500]; char. 54: 1→2 [0.600]
node_15 → node_16	1	char. 55: 0→1 [1.000]
node_16 → Ascalobyas microcerus	2	char. 23: 0→2 [1.000]; char. 74: 5→4 [1.000]
node_16 → Ascalobyas oswaldi	2	char. 10: 0→5 [1.000]; char. 43: 5→4 [0.357]
node_15 → node_17	6	char. 10: 0→1 [1.000]; char. 24: 0→3 [0.750]; char. 29: 3→0 [0.500]; char. 35: 0→1 [0.600]; char. 39: 2→3 [1.000]; char. 75: 2→1 [0.714]
node_17 → Haploglenius procerus	2	char. 34: 1→2 [0.400]; char. 44: 1→2 [0.333]
node_17 → node_18	2	char. 7: 1→2 [0.500]; char. 19: 0→1 [0.333]
node_18 → Haploglenius peruvianus	3	char. 5: 2→1 [0.429]; char. 29: 0→1 [0.500]; char. 70: 0→1 [0.750]
node_18 → node_19	3	char. 11: 0→3 [1.000]; char. 54: 2→1 [0.600]; char. 67: 0→1 [0.400]
node_19 → node_20	2	char. 8: 0→2 [0.750]; char. 76: 5→0 [0.727]
node_20 → Haploglenius costatus	0	no unambiguous character changes
node_20 → node_21	2	char. 35: 1→2 [0.600]; char. 75: 1→3 [0.714]
node_21 → node_22	5	char. 15: 1→0 [0.200]; char. 28: 0→1 [0.500]; char. 36: 2→3 [0.600]; char. 44: 1→0 [0.333]; char. 56: 1→0 [0.200]

Table 2. List of unambiguous apomorphies, by branch, cont.

branch	# changes	apomorphic character change(s)
node_22 → node_23	3	char. 6: 2→3 [0.600]; char. 20: 0→2 [0.500]; char. 26: 2→4 [0.667]
node_23 → Haploglenius acuminatus	8	char. 27: 2→5 [0.500]; char. 35: 2→3 [0.600]; char. 42: 0→2 [1.000]; char. 43: 4→5 [0.357]; char. 47: 0→1 [1.000]; char. 50: 0→2 [0.750]; char. 51: 1→3 [0.600]; char. 52: 1→0 [0.667]; char. 54: 1→0 [0.600]
node_23 → Haploglenius gerstaeckeri	2	char. 29: 7→6 [0.500]; char. 36: 3→1 [0.600]
node_22 → node_24	20	char. 8: 2→3 [0.750]; char. 9: 0→1 [1.000]; char. 11: 3→2 [1.000]; char. 17: 1→3 [0.750]; char. 21: 5→4 [0.857]; char. 23: 0→3 [1.000]; char. 24: 3→2 [0.750]; char. 38: 0→1 [0.400]; char. 49: 1→0 [0.500]; char. 51: 1→2 [0.600]; char. 53: 1→2 [0.750]; char. 61: 3→7 [0.875]; char. 62: 3→7 [1.000]; char. 67: 1→2 [0.400]; char. 68: 0→2 [1.000]; char. 71: 3→1 [0.750]; char. 72: 1→0 [0.333]; char. 73: 2→3 [1.000]; char. 74: 5→6 [1.000]; char. 75: 3→5 [0.714]; char. 76: 0→7 [0.727]
node_24 → Haploglenius elongatus	3	char. 5: 2→1 [0.429]; char. 45: 1→0 [0.333]; char. 59: 1→2 [1.000]
node_24 → node_25	5	char. 10: 1→3 [1.000]; char. 12: 1→0 [0.250]; char. 26: 2→1 [0.667]; char. 32: 0→2 [1.000]; char. 58: 0→1 [1.000]
node_25 → Haploglenius appendiculatus	0	no unambiguous character changes
node_25 → Haploglenius juvenilis	2	char. 61: 7→6 [0.875]; char. 76: 7→6 [0.727]
node_19 → node_26	5	char. 5: 2→3 [0.429]; char. 14: 7→B [0.688]; char. 25: 3→2 [0.571]; char. 69: 1→3 [0.429]; char. 70: 0→3 [0.750]
node_26 → Haploglenius luteus	1	char. 32: 0→1 [1.000]
node_26 → node_27	2	char. 64: 0→1 [0.500]; char. 77: 2→3 [0.750]
node_27 → Haploglenius neoguineensis	2	char. 6: 2→1 [0.600]; char. 46: 0→1 [0.333]
node_27 → node_28	5	char. 12: 1→0 [0.250]; char. 14: B→9 [0.688]; char. 15: 1→0 [0.200]; char. 70: 3→2 [0.750]; char. 75: 1→4 [0.714]
node_28 → node_29	2	char. 24: 3→0 [0.750]; char. 69: 3→1 [0.429]
node_29 → Haploglenius handlirschi	5	char. 6: 2→1 [0.600]; char. 14: 9→0 [0.688]; char. 43: 4→5 [0.357]; char. 52: 1→2 [0.667]; char. 70: 2→1 [0.750]
node_29 → node_30	3	char. 10: 1→4 [1.000]; char. 46: 0→1 [0.333]; char. 64: 1→0 [0.500]
node_30 → Haploglenius aquilonius	1	char. 27: 1→2 [0.500]
node_30 → node_31	2	char. 18: 0→3 [02.600]; char. 49: 1→0 [0.500]
node_31 → Haploglenius reticulatus	1	char. 69: 1→2 [0.429]
node_31 → Haploglenius abdominevittatus	8	char. 5: 3→2 [0.429]; char. 12: 0→1 [0.250]; char. 15: 0→1 [0.200]; char. 21: 5→6 [0.857]; char. 26: 2→3 [0.667]; char. 27: 1→3 [0.500]; char. 33: 0→1 [1.000]; char. 34: 2→1 [0.400]; char. 44: 1→0 [0.333]
node_28 → node_32	2	char. 5: 3→2 [0.429]; char. 65: 0→1 [1.000]
node_32 → node_33	4	char. 18: 0→3 [0.600]; char. 28: 0→1 [0.500]; char. 36: 2→1 [0.600]; char. 51: 1→2 [0.600]
node_33 → Haploglenius angulatus	1	char. 43: 4→2 [0.357]
node_33 → Haploglenius flavicornis	0	no unambiguous character changes
node_32 → node_34	5	char. 14: 9→6 [0.688]; char. 25: 2→3 [0.571]; char. 43: 4→5 [0.357]; char. 54: 1→3 [0.600]; char. 56: 1→0 [0.200]
node_34 → node_35	2	char. 20: 0→1 [0.500]; char. 53: 1→3 [0.750]
node_35 → Haploglenius extensus	3	char. 8: 0→1 [0.750]; char. 29: 0→5 [0.500]; char. 50: 0→2 [0.750]
node_34 → node_36	3	char. 11: 3→4 [1.000]; char. 40: 0→1 [1.000]; char. 50: 0→3 [0.750]
node_36 → Haploglenius decorus	3	char. 14: 6→0 [0.688]; char. 41: 0→1 [1.000]; char. 46: 0→1 [0.333]
node_13 → node_14	2	char. 30: 0→1 [0.500]; char. 31: 0→1 [1.000]
node_14 → Neascalobyas machadoi	3	char. 1: 0→1 [0.250]; char. 26: 2→1 [0.667]; char. 38: 0→1 [0.400]
node_14 → Neascalobyas nigrantia	4	char. 4: 0→1 [0.250]; char. 5: 2→3 [0.429]; char. 10: 0→2 [1.000]; char. 75: 2→1 [0.714]

Table 3. List of character state changes, by character. Character states transformations as optimized by PAUP* on the topology obtained in the cladistic analysis (A3 Fig. 1) are presented here. Optimizations are provided in the format [node#: ancestral state→derived state node#/terminal taxon]. Node numbers correspond to those found on A3 Fig. 1. Both unambiguous (→) and ambiguous (-->>) character state changes are provided.

char#	CI	steps	state transformation(s)
1	0.250	4	node 4 0 → 1 node 5; node 20: 0 -->> 1 node 21; node 22: 1 -->> 0 node 24; node 14: 0 → 1 Neascalobyas machadoi
2	1.000	1	node 2: 0 → 1 node 3
3	1.000	2	node 1: 1 → 0 Albardia furcata; node 2: 1 → 2 node 3
4	0.500	2	node 2: 0 → 1 Protidricerus elwesii; node 14: 0 → 1 Neascalobyas nigrantia
5	0.429	7	node 2: 0 → 2 node 3; node 18: 2 → 1 Haploglenius peruvianus; node 24: 2 → 1 Haploglenius elongatus; node 19: 2 → 3 node 26; node 31: 3 → 2 Haploglenius abdominevittatus; node 28: 3 → 2 node 32; node 14: 2 → 3 Neascalobyas nigrantia
6	0.600	5	node 1: 1 → 0 Albardia furcata; node 2: 1 → 2 node 3; node 22: 2 → 3 node 23; node 27: 2 → 1 Haploglenius neoguineensis; node 29: 2 → 1 Haploglenius handlirschi
7	0.500	4	node 1: 2 → 0 Albardia furcata; node 3: 2 → 1 node 13; node 17: 1 → 2 node 18; node 22: 2 -->> 1 node 24
8	0.750	4	node 1: 1 → 0 node 2; node 19: 0 → 2 node 20; node 22: 2 → 3 node 24; node 35: 0 → 1 Haploglenius extensus
9	1.000	1	node 22: 0 → 1 node 24
10	1.000	5	node 16: 0 → 5 Ascalobyas oswaldi; node 15: 0 → 1 node 17; node 24: 1 → 3 node 25; node 29: 1 → 4 node 30; node 14: 0 → 2 Neascalobyas nigrantia
11	1.000	4	node 1: 0 → 1 Allocormodes nigristigma; node 18: 0 → 3 node 19; node 22: 3 → 2 node 24; node 34: 3 → 4 node 36
12	0.250	4	node 3: 0 → 1 node 13; node 24: 1 → 0 node 25; node 27: 1 → 0 node 28; node 31: 0 → 1 Haploglenius abdominevittatus
13	0.500	2	node 3: 0 -->> 1 node 13; node 15: 1 -->> 0 node 17
14	0.688	16	node 1: 0 -->> 8 Albardia furcata; node 1: 0 -->> 2 Allocormodes nigristigma; node 2: 0 -->> 1 node 3; node 6: 1 → 0 Amoea iniqua; node 3: 1 -->> 3 node 13; node 15: 3 -->> 7 node 17; node 20: 7 -->> 0 node 21; node 21: 0 -->> 6 node 22; node 22: 6 -->> A node 23; node 19: 7 → B node 26; node 27: B → 9 node 28; node 29: 9 → 0 Haploglenius handlirschi; node 32: 9 → 6 node 34; node 36: 6 → 0 Haploglenius decoratus; node 13: 3 -->> 4 node 14; node 14: 4 -->> 5 Neascalobyas nigrantia
15	0.200	5	node 3: 0 -->> 1 node 13; node 21: 1 → 0 node 22; node 27: 1 → 0 node 28; node 31: 0 → 1 Haploglenius abdominevittatus; node 14: 1 -->> 0 Neascalobyas nigrantia
16	0.500	2	node 19: 0 -->> 1 node 26; node 27: 1 -->> 0 node 28
17	0.750	4	node 1: 1 → 0 Albardia furcata; node 8: 1 → 2 node 11; node 5: 1 → 2 Amoea chlorops; node 22: 1 → 3 node 24
18	0.600	5	node 1: 0 → 1 Allocormodes nigristigma; node 22: 0 -->> 2 node 24; node 24: 2 -->> 3 Haploglenius elongatus; node 30: 0 → 3 node 31; node 32: 0 → 3 node 33
19	0.333	3	node 1: 0 → 1 Allocormodes nigristigma; node 3: 0 → 1 node 4; node 17: 0 → 1 node 18
20	0.500	4	node 9: 0 → 1 node 10; node 22: 0 → 2 node 23; node 24: 0 -->> 1 node 25; node 34: 0 → 1 node 35
21	0.857	7	node 2: 0 -->> 3 node 3; node 5: 3 → 2 node 6; node 7: 2 → 1 node 8; node 15: 3 -->> 5 node 17; node 22: 5 → 4 node 24; node 31: 5 → 6 Haploglenius abdominevittatus; node 13: 3 -->> 0 node 14:
22	1.000	1	node 10: 0 → 1 Amoea impediens
23	1.000	3	node 10: 0 → 1 Amoea impediens; node 16: 0 → 2 Ascalobyas microcerus; node 22: 0 → 3 node 24
24	0.750	4	node 8: 0 → 1 node 11; node 15: 0 → 3 node 17; node 22: 3 → 2 node 24; node 28: 3 → 0 node 29
25	0.571	7	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 2: 2 -->> 3 node 3; node 21: 3 -->> 2 node 22; node 22: 2 -->> 4 node 23; node 19: 3 → 2 node 26; node 32: 2 → 3 node 34
26	0.667	6	node 1: 0 → 1 Allocormodes nigristigma; node 2: 0 → 2 node 3; node 22: 2 → 4 node 23; node 24: 2 → 1 node 25; node 31: 2 → 3 Haploglenius abdominevittatus; node 14: 2 → 1 Neascalobyas machadoi
27	0.500	12	node 1: 0 → 6 Albardia furcata; node 2: 0 → 1 Protidricerus elwesii; node 18: 0 -->> 1 node 19; node 19: 1 -->> 2 node 20; node 23: 2 → 5 Haploglenius acuminatus; node 22: 2 -->> 3 node 24; node 24: 3 -->> 4 node 25; node 30: 1 → 2 Haploglenius aquilonius; node 31: 1 → 3 Haploglenius abdominevittatus; node 28: 1 -->> 0 node 32; node 32: 0 -->> 3 node 33; node 35: 0 -->> 1 Haploglenius extensus
28	0.500	2	node 21: 0 → 1 node 22; node 32: 0 → 1 node 33

Table 3. List of character state changes, by character, cont.

char. #	CI	steps	state transformation(s)
29	0.500	14	node 1: 0 → 3 node 2; node 5: 3 → 2 node 6; node 7: 2 → 4 Amoea nivea; node 15: 3 → 0 node 17; node 18: 0 → 1 Haploglenius peruvianus; node 20: 0 -->> 1 node 21; node 21: 1 -->> 7 node 22; node 23: 7 → 6 Haploglenius gerstaeckeri; node 28: 0 -->> 1 node 29; node 30: 1 -->> 0 node 31; node 31: 0 -->> 5 Haploglenius abdominevittatus; node 32: 0 -->> 5 node 33; node 33: 5 -->> 6 Haploglenius flavicornis; node 35: 0 → 5 Haploglenius extensus
30	0.500	2	node 1: 0 → 1 Allocormodes nigristigma; node 13: 0 → 1 node 14
31	1.000	1	node 13: 0 → 1 node 14
32	1.000	2	node 24: 0 → 2 node 25; node 26: 0 → 1 Haploglenius luteus
33	1.000	1	node 31: 0 → 1 Haploglenius abdominevittatus
34	0.400	5	node 1: 0 → 1 node 2; node 17: 1 → 2 Haploglenius procerus; node 27: 1 -->> 2 node 28; node 31: 2 → 1 Haploglenius abdominevittatus; node 32: 2 -->> 1 node 33
35	0.600	5	node 15: 0 → 1 node 17; node 20: 1 → 2 node 21; node 23: 2 → 3 Haploglenius acuminatus; node 28: 1 -->> 0 node 32; node 33: 0 -->> 1 Haploglenius flavicornis
36	0.600	5	node 1: 1 → 0 Albardia furcata; node 13: 1 -->> 2 node 15; node 21: 2 → 3 node 22; node 23: 3 → 1 Haploglenius gerstaeckeri; node 32: 2 → 1 node 33
37	1.000	1	node 1: 1 → 0 Allocormodes nigristigma
38	0.400	5	node 1: 0 → 2 Albardia furcata; node 2: 0 → 1 Protidricerus elwesii; node 9: 0 → 1 node 10; node 22: 0 → 1 node 24; node 14: 0 → 1 Neascalobyas machadoi
39	1.000	5	node 1: 0 → 1 Allocormodes nigristigma; node 2: 0 → 2 node 3; node 15: 2 → 3 node 17; node 34: 3 -->> 4 node 36; node 36: 4 -->> 5 Haploglenius decorus
40	1.000	1	node 34: 0 → 1 node 36
41	1.000	1	node 36: 0 → 1 Haploglenius decoratus
42	1.000	2	node 2: 0 → 1 Protidricerus elwesii; node 23: 0 → 2 Haploglenius acuminatus
43	0.357	14	node 1: 2 → 3 Albardia furcata; node 2: 2 → 0 node 3; node 6: 0 → 2 node 7; node 8: 2 → 1 node 11; node 12: 1 → 0 Amoea periculosa; node 10: 2 → 0 Amoea arenosa; node 13: 0 → 5 node 15; node 16: 5 → 4 Ascalobyas oswaldi; node 34: 3 -->> 4 node 36; node 36: 4 -->> 5 Haploglenius decorus; node 23: 4 → 5 Haploglenius acuminatus; node 29: 4 → 5 Haploglenius handlirschi; node 33: 4 → 2 Haploglenius latipennis; node 32: 4 → 5 node 34
44	0.333	6	node 1: 0 -->> 2 Allocormodes nigristigma; node 1: 0 -->> 1 node 2; node 17: 1 → 2 Haploglenius procerus; node 21: 1 → 0 node 22; node 31: 1 → 0 Haploglenius abdominevittatus; node 32: 1 -->> 0 node 33
45	0.333	3	node 4: 0 → 1 Amoea immaculata; node 13: 0 → 1 node 15; node 24: 1 → 0 Haploglenius elongatus
46	0.333	3	node 27: 0 → 1 Haploglenius neoguineensis; node 29: 0 → 1 node 30; node 36: 0 → 1 Haploglenius decoratus
47	1.000	1	node 23: 0 → 1 Haploglenius acuminatus
48	1.000	1	node 12: 0 → 1 Amoea latipennis
49	0.500	4	node 1: 0 → 2 Allocormodes nigristigma; node 13: 0 → 1 node 15; node 22: 1 → 0 node 24; node 30: 1 → 0 node 31
50	0.750	4	node 1: 0 → 1 Allocormodes nigristigma; node 23: 0 → 2 Haploglenius acuminatus; node 35: 0 → 2 Haploglenius extensus; node 34: 0 → 3 node 36
51	0.600	5	node 1: 0 -->> 3 Allocormodes nigristigma; node 1: 0 -->> 1 node 2; node 23: 1 → 3 Haploglenius acuminatus; node 22: 1 → 2 node 24; node 32: 1 → 2 node 33
52	0.667	3	node 1: 0 → 1 node 2; node 23: 1 → 0 Haploglenius acuminatus; node 29: 1 → 2 Haploglenius handlirschi
53	0.750	4	node 1: 0 -->> 1 Allocormodes nigristigma; node 2: 0 -->> 1 node 3; node 22: 1 → 2 node 24; node 34: 1 → 3 node 35
54	0.600	5	node 1: 0 → 1 node 2; node 13: 1 → 2 node 15; node 18: 2 → 1 node 19; node 23: 1 → 0 Haploglenius acuminatus; node 32: 1 → 3 node 34
55	1.000	1	node 15: 0 → 1 node 16
56	0.200	5	node 13: 0 -->> 1 node 15; node 17: 1 -->> 0 Haploglenius procerus; node 21: 1 → 0 node 22; node 30: 1 -->> 0 node 31; node 32: 1 → 0 node 34
57	1.000	6	node 2: 0 -->> 1 node 3; node 12: 1 → 2 Amoea latipennis; node 3: 1 -->> 3 node 13; node 22: 3 -->> 4 node 24; node 24: 4 -->> 6 Haploglenius elongatus; node 25: 4 -->> 5 Haploglenius appendiculatus
58	1.000	1	node 24: 0 → 1 node 25
59	1.000	2	node 2: 0 → 1 node 3; node 24: 1 → 2 Haploglenius elongatus
60	0.857	7	node 1: 1 → 0 Albardia furcata; node 2: 1 → 3 node 3; node 11: 3 → 2 node 12; node 9: 3 → 2 node 10; node 7: 3 → 4 Amoea nivea; node 21: 3 -->> 5 node 22; node 22: 5 -->> 6 node 23

Table 3. List of character state changes, by character, cont.

char. #	CI	steps	state transformation(s)
61	0.875	8	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 2: 2 -->> 3 node 3; node 6: 3 -->> 4 node 7; node 7: 4 -->> 5 node 8; node 8: 5 -->> 6 node 11; node 22: 3 → 7 node 24; node 25: 7 → 6 Haploglenius juvenilis
62	1.000	7	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 2: 2 -->> 3 node 3; node 6: 3 -->> 4 node 7; node 7: 4 -->> 6 node 8; node 11: 6 → 5 Amoea flavitaenia; node 22: 3 → 7 node 24
63	1.000	2	node 24: 0 -->> 1 node 25; node 25: 1 -->> 2 Haploglenius juvenilis
64	0.500	2	node 26: 0 → 1 node 27; node 29: 1 → 0 node 30
65	1.000	1	node 28: 0 → 1 node 32
66	1.000	2	node 28: 0 -->> 1 node 32; node 32: 1 -->> 2 node 33
67	0.400	5	node 7: 0 -->> 2 node 8; node 11: 2 -->> 0 node_39; node 4: 0 → 2 Amoea immaculata; node 18: 0 → 1 node 19; node 22: 1 → 2 node 24
68	1.000	2	node 1: 0 → 1 Allocormodes nigristigma; node 22: 0 → 2 node 24
69	0.429	7	node 17: 0 -->> 1 node 18; node 20: 1 -->> 0 node 21; node 19: 1 → 3 node 26; node 28: 3 → 1 node 29; node 31: 1 → 2 Haploglenius reticulatus; node 32: 3 -->> 2 node 34; node 36: 2 -->> 3 Haploglenius decorus
70	0.750	4	node 18: 0 → 1 Haploglenius peruvianus; node 19: 0 → 3 node 26; node 27: 3 → 2 node 28; node 29: 2 → 1 Haploglenius handlirschi
71	0.750	4	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 3: 2 → 3 node 13; node 22: 3 → 1 node 24
72	0.333	3	node 2: 0 → 1 node 3; node 12: 1 → 0 Amoea latipennis; node 22: 1 → 0 node 24
73	1.000	3	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 22: 2 → 3 node 24
74	1.000	6	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 2: 2 -->> 3 node 3; node 3: 3 -->> 5 node 13; node 16: 5 → 4 Ascalobyas microcerus; node 22: 5 → 6 node 24
75	0.714	7	node 1: 2 → 0 Albardia furcata; node 6: 2 → 1 Amoea iniqua; node 15: 2 → 1 node 17; node 20: 1 → 3 node 21; node 22: 3 → 5 node 24; node 27: 1 → 4 node 28; node 14: 2 → 1 Neascalobyas nigrantia
76	0.727	11	node 1: 0 -->> 1 node 2; node 2: 1 -->> 2 node 3; node 11: 2 → 4 node 12; node 8: 2 → 3 node 9; node 3: 2 -->> 5 node 13; node 17: 5 -->> 2 Haploglenius procerus; node 19: 5 → 0 node 20; node 22: 0 → 7 node 24; node 25: 7 → 6 Haploglenius juvenilis; node 28: 5 -->> 0 node 29; node 29: 0 -->> 8 node 30
77	0.750	4	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 3: 2 -->> 3 node_47; node 26: 2 → 3 node 27
78	1.000	2	node 1: 1 → 0 Albardia furcata; node 2: 1 → 2 node 3
79	0.667	3	node 1: 0 -->> 1 Allocormodes nigristigma; node 1: 0 -->> 2 node 2; node 22: 2 -->> 0 node 24

APPENDIX 4

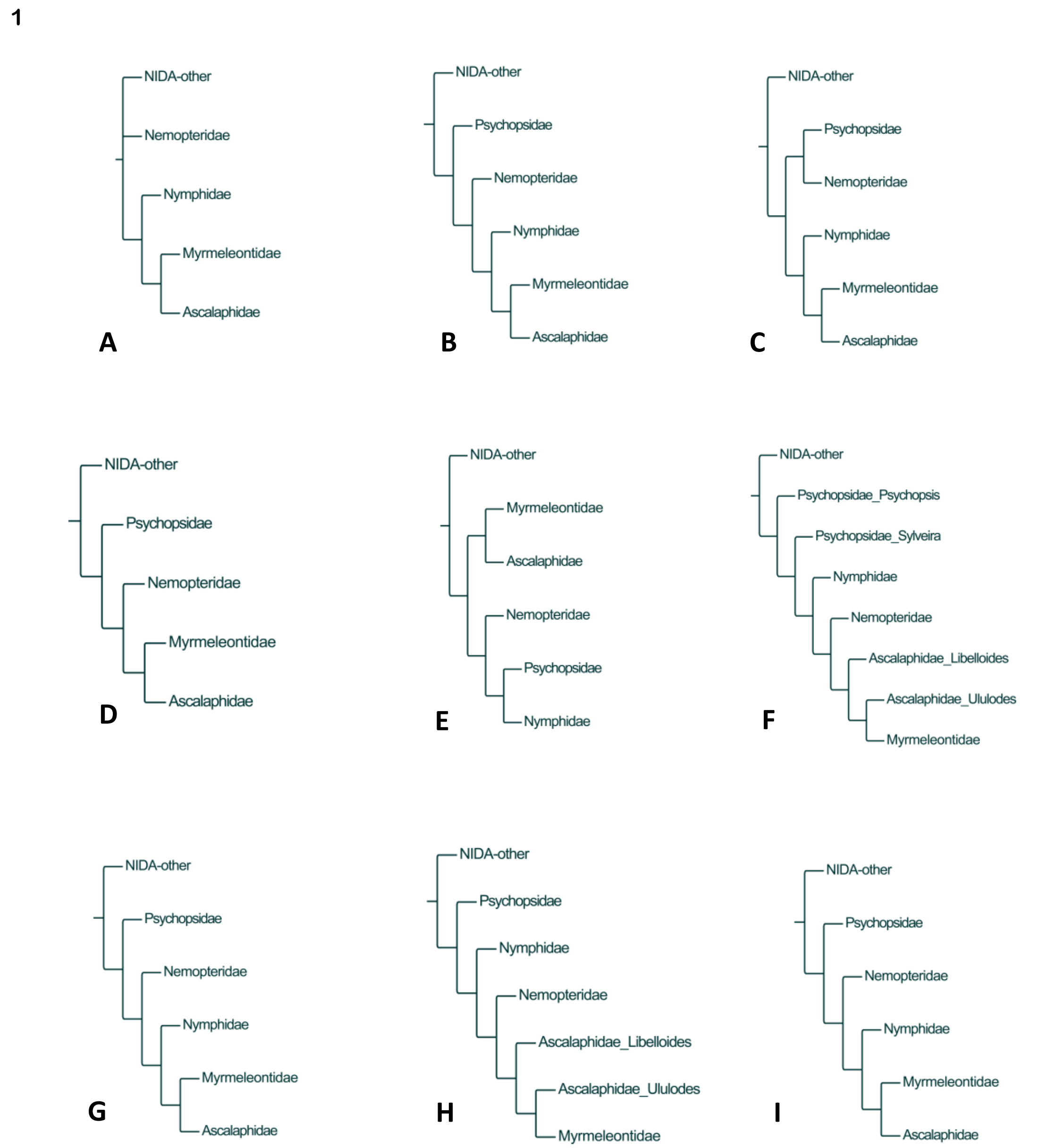


Fig. 1, A-I.—Phylogenetic hypotheses for the families of Myrmeleontiformia. A, Handlirsch (1906-1908). B, Withycombe (1925). C, Aspöck et al. (2001). D, Haring and Aspöck (2004). E, Aspöck and Aspöck (2008). F-I, Winterton (2010): F, parsimony of combined molecular data; G, parsimony of morphological data; H, parsimony of combined molecular and morphology; I, Bayesian of combined molecular and morphology. NIDA = Neuropterida.

2

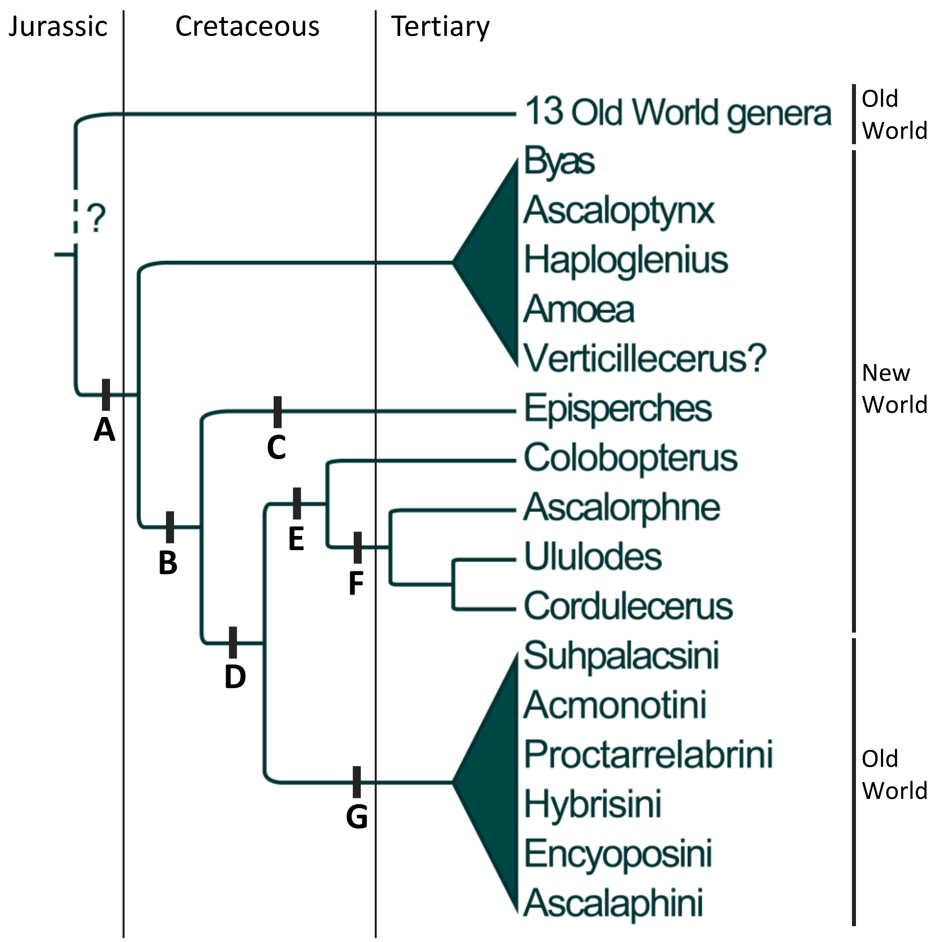


Fig. 2.—Henry's (1978b) phylogenetic hypothesis for Ascalaphidae based on optimization of adult eyes, ovarioles, and repagula (reproduced from his fig. 1). A=abortive eggs with trophic functions, 12+12 ovarioles. B=abortive eggs modified into primitive barriers. C=ovarioles reduced to 10+12. D=divided eye. E=eggs become true repagula (ant barriers). F=repagula become reduced in size. G=loss of abortive eggs, 10+0 ovarioles.

3

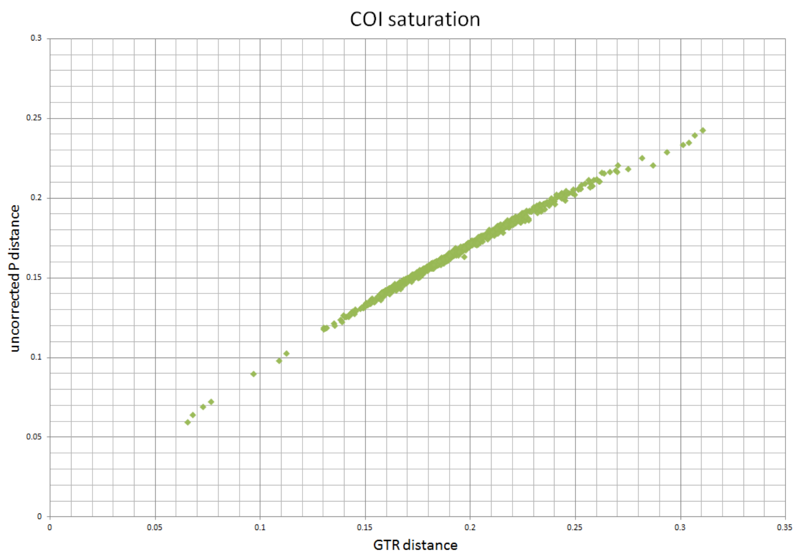


Fig. 3.—The COI data partition was explored for saturation. Uncorrected P and GTR distances were generated in PAUP* and plotted against each other. Each point represents a pairwise comparison between two taxa. $R^2 = 0.9948$; $y = 0.7186x + 0.026$. Saturation in this dataset is present but almost negligible.

4

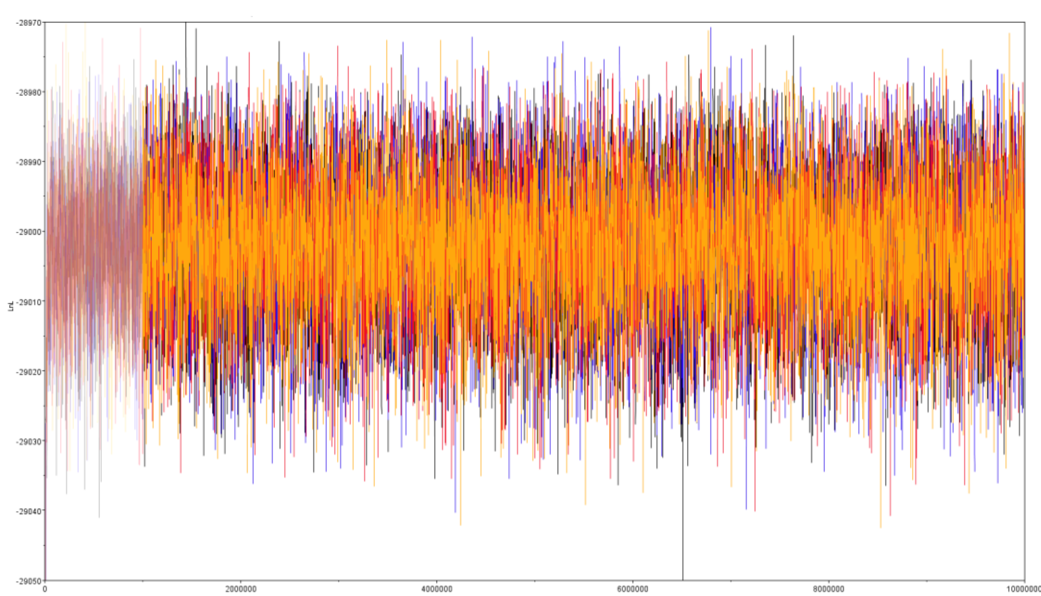


Fig. 4.—Chromatograph illustrating stationarity in all chains of the Bayesian analysis. The analysis was run for 10 million generations on the CIPRES cluster. Burn-in occurred early during the one million cycle burn-in period indicated by the dulled-out left hand portion of the figure.

5

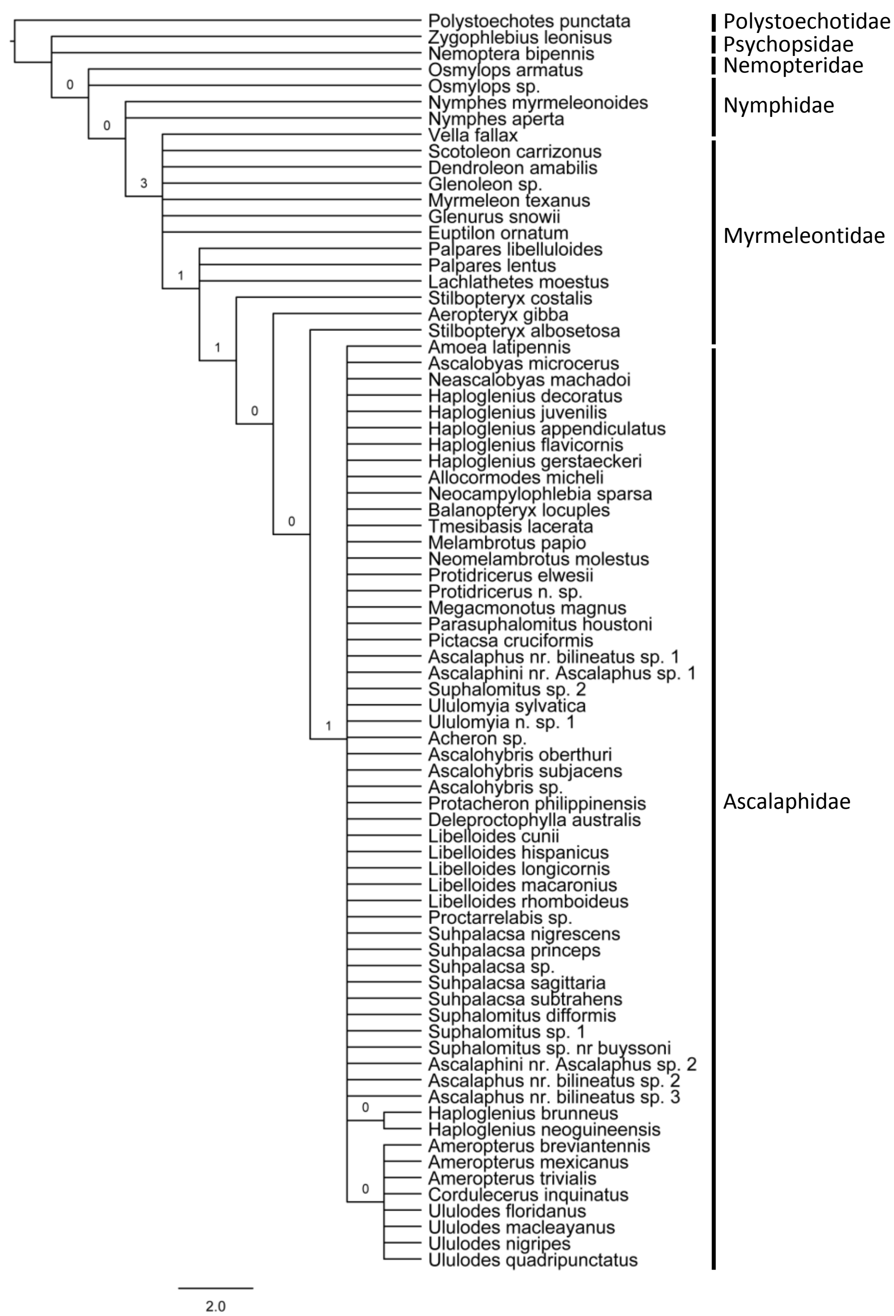


Fig. 5.—Strict consensus cladogram from parsimony analysis of morphology dataset, from 6 trees. Bremer support values are provided to the left of the nodes to which they correspond. The scale at bottom indicates branch length.

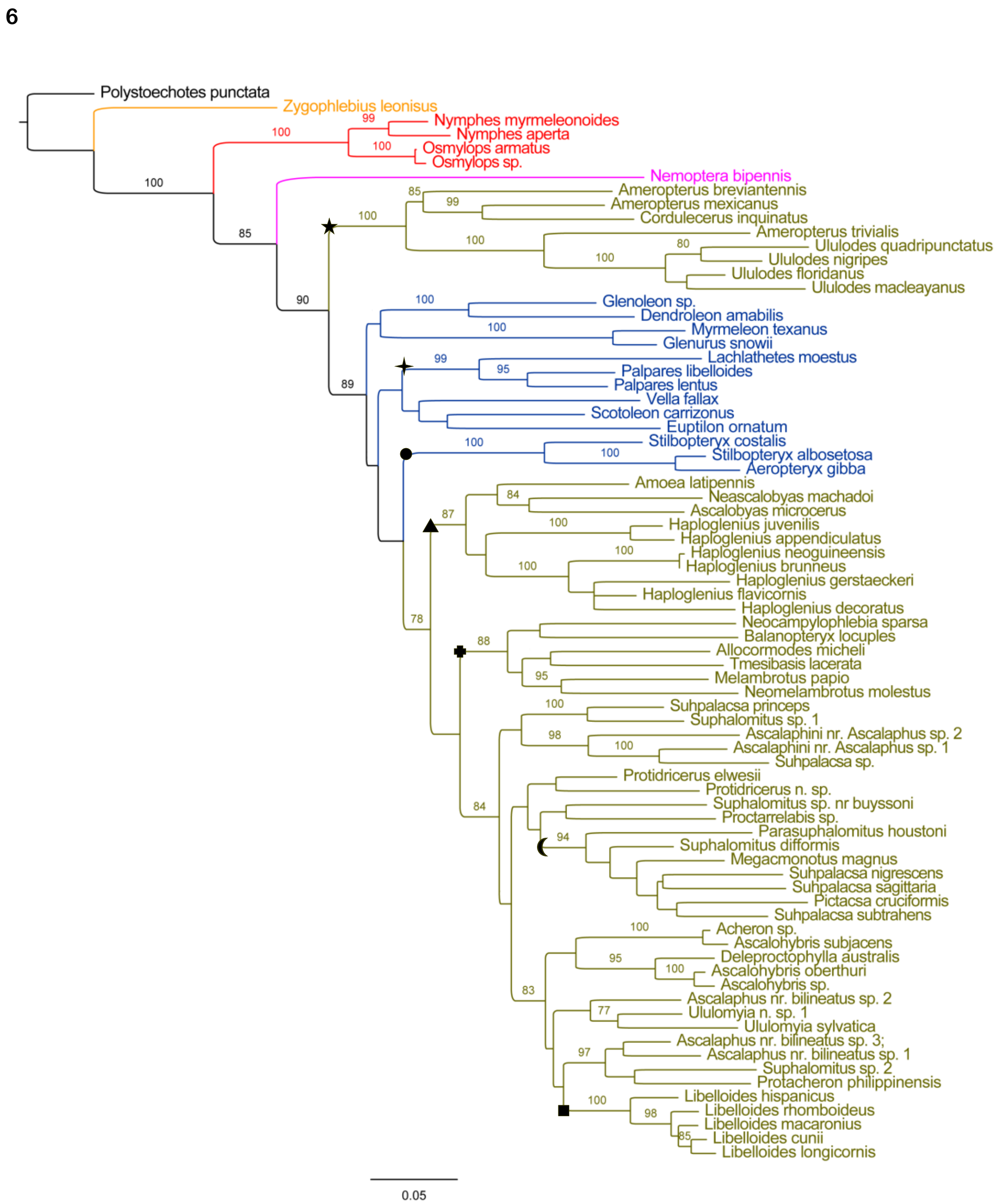


Fig. 6.—Phylogram of molecular data from maximum likelihood analysis. Families are indicated by color: Polystoechotidae-black (outgroup); Psychopsidae-orange; Nymphidae-red; Nemopteridae-pink; Myrmeleontidae-blue; Ascalaphidae-green. Groups of special interest are marked with symbols on their defining nodes: Ululodini [5-pointed star]; Palparinae [4-pointed star]; Stilbopteryginae [circle]; New World Haplogleniinae [triangle]; African Haplogleniinae [cross]; Australian Suhpalacsini [half-moon]; *Libelloides* [square]. Both Ascalaphidae and Myrmeleontidae were recovered as paraphyletic. Bootstrap support values are provided to the left of the nodes to which they correspond (those below 75 are not reported). The scale at bottom indicates branch length.

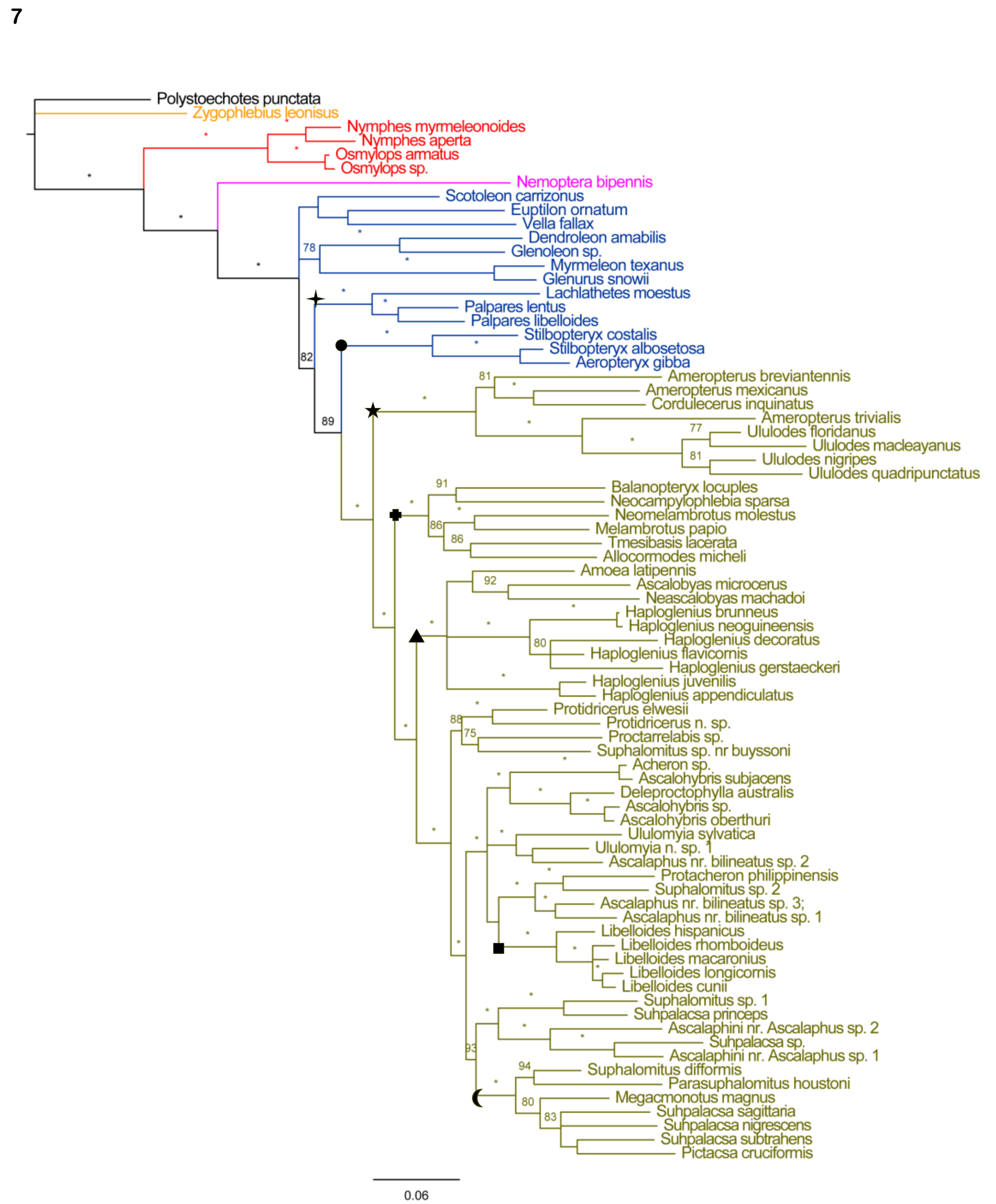


Fig. 7.—Total evidence phylogram of morphology and molecular data from Bayesian analysis. Families are indicated by color, and groups of special interest are marked with symbols, as in Fig. 6. Myrmeleontidae were recovered as paraphyletic, and Ascalaphidae monophyletic. Posterior probability values are provided to the left of the nodes to which they correspond: values above 95 are represented by an asterisk (*); those below 75 are not included. The scale at bottom indicates branch length.

8

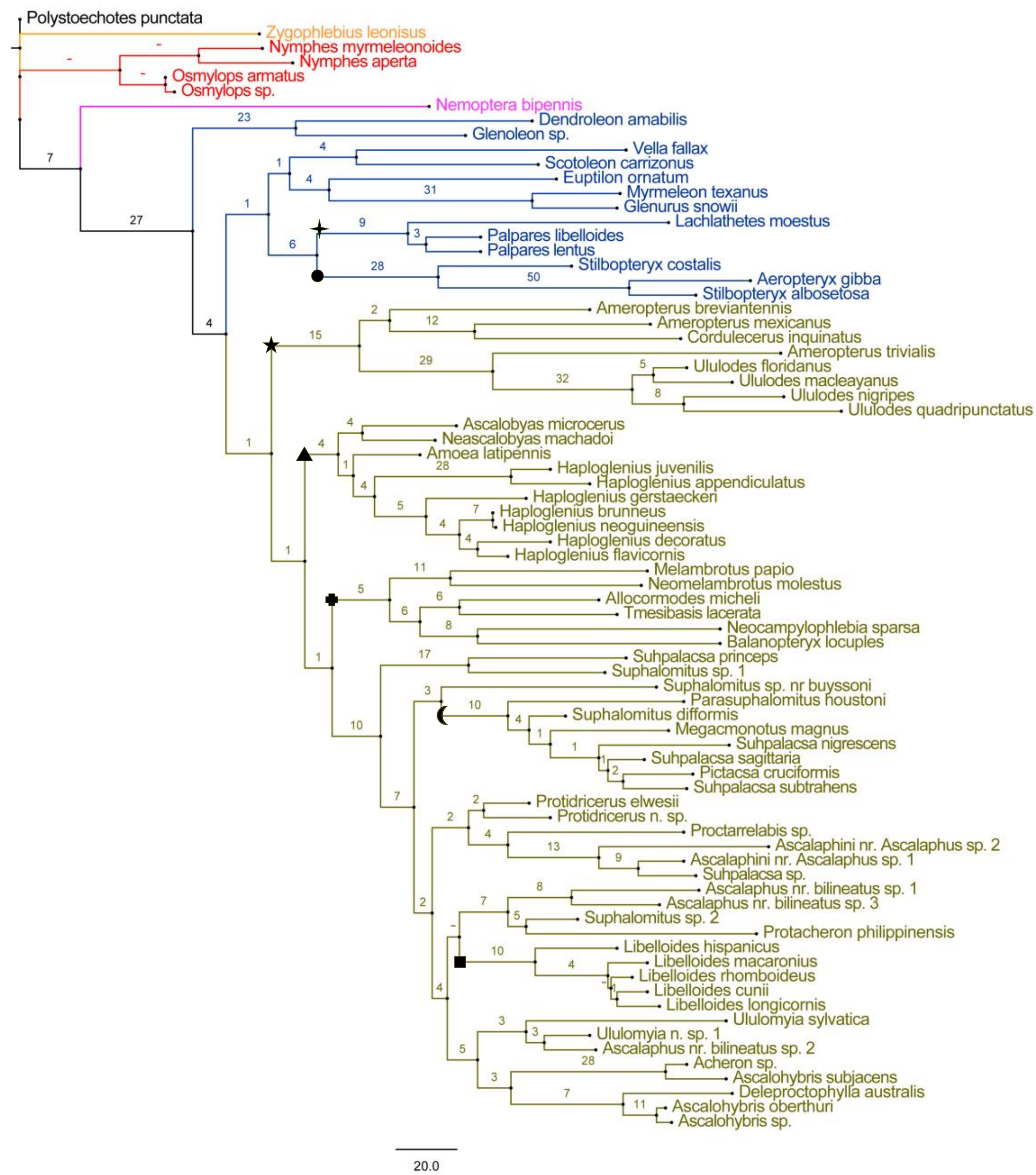


Fig. 8.—Total evidence phylogram of morphology and molecular data from parsimony analysis. Families are indicated by color, and groups of special interest are marked with symbols, as in Fig. 6. All families were recovered as monophyletic except for Myrmeleontidae. Bremer support values are provided to the left of the nodes to which they correspond. Nodes without Bremer support are indicated with a dash (-). The scale at bottom indicates branch length.

9

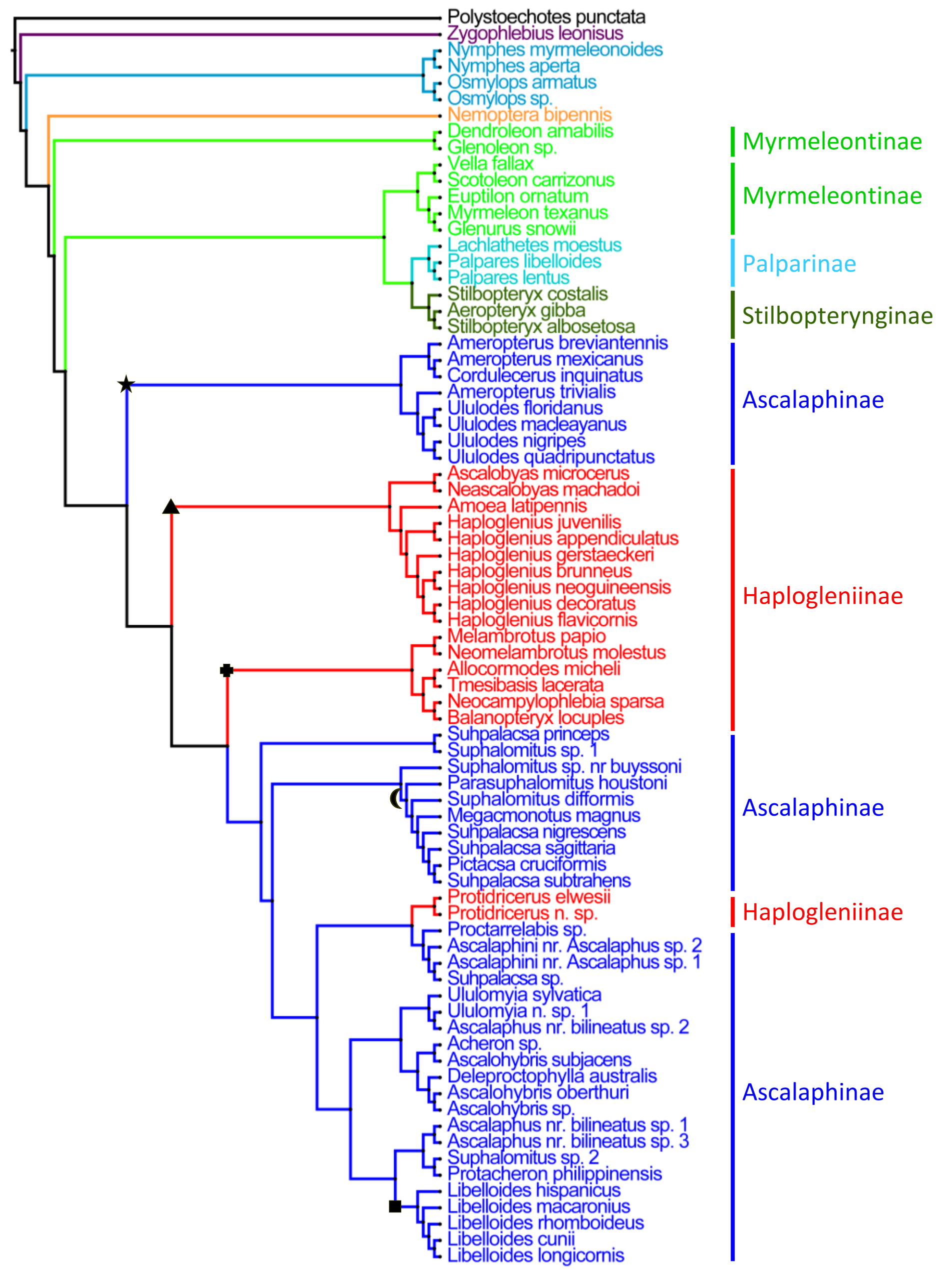


Fig. 9.—Parsimony cladogram color-coded to indicate subfamily boundaries under current definitions. Infra-subfamilial groups of special interest are marked with symbols, as in Fig. 6. Myrmeleontinae was paraphyletic in all analyses with respect to Dendroleontini (see Fig. 10). Ascalaphinae was paraphyletic in all analyses with respect to Ululodini. Haplogleniinae was also paraphyletic in all analyses, separating into three clades.

10

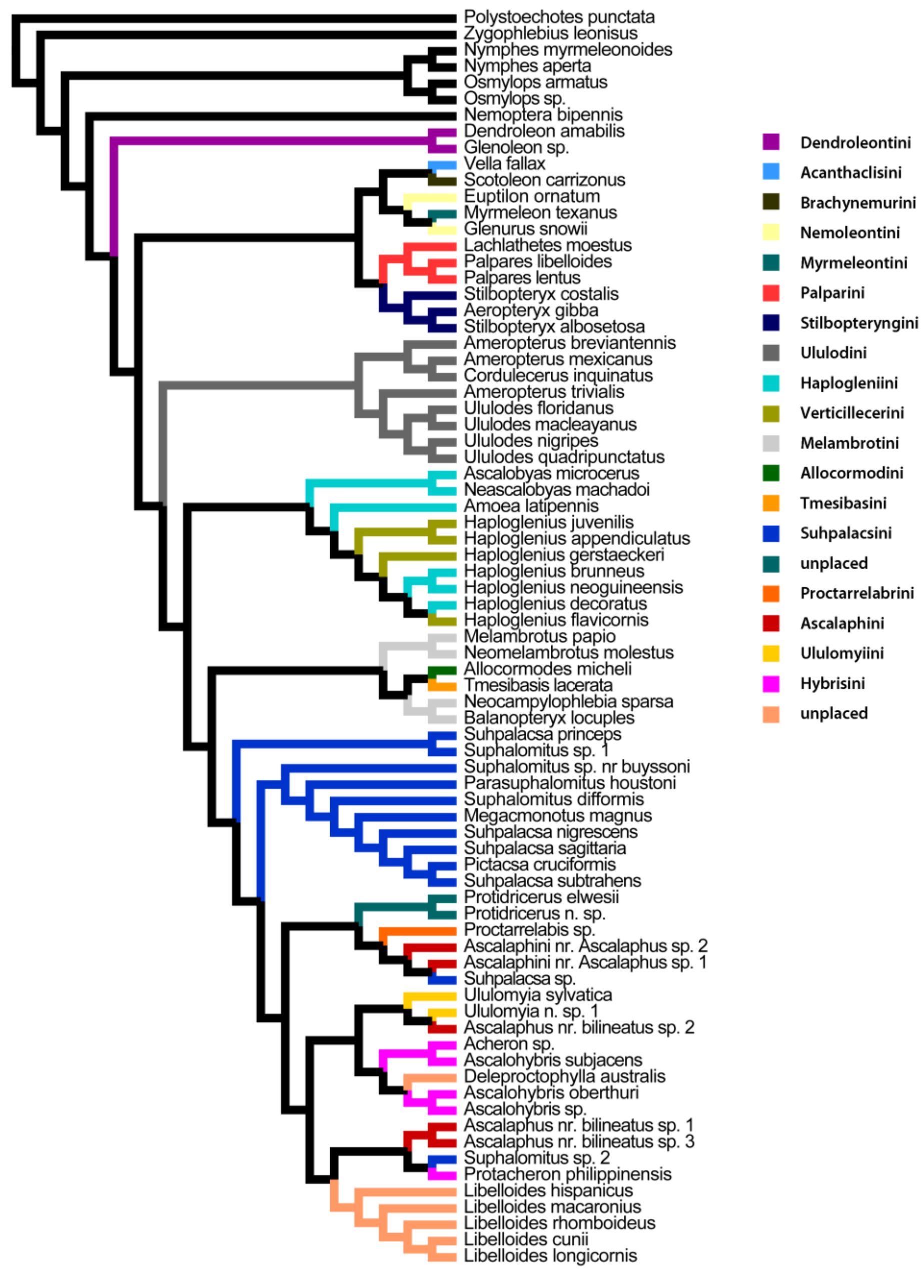


Fig. 10.—Parsimony cladogram color-coded to indicate tribal organization under current definitions. Within Myrmeleontidae, only Dendroleontini, Palparini, and Stilbopterygini were monophyletic. In Ascalaphidae, only Ululodini was monophyletic in all analyses, with all other tribes para- or polyphyletic. Tribes such as Verticilllecerini, Haplogleniini, Melambrotini, Suhpalacsini, Ascalaphini, and Hybrisini are para- and polyphyletic and should be redefined.

11

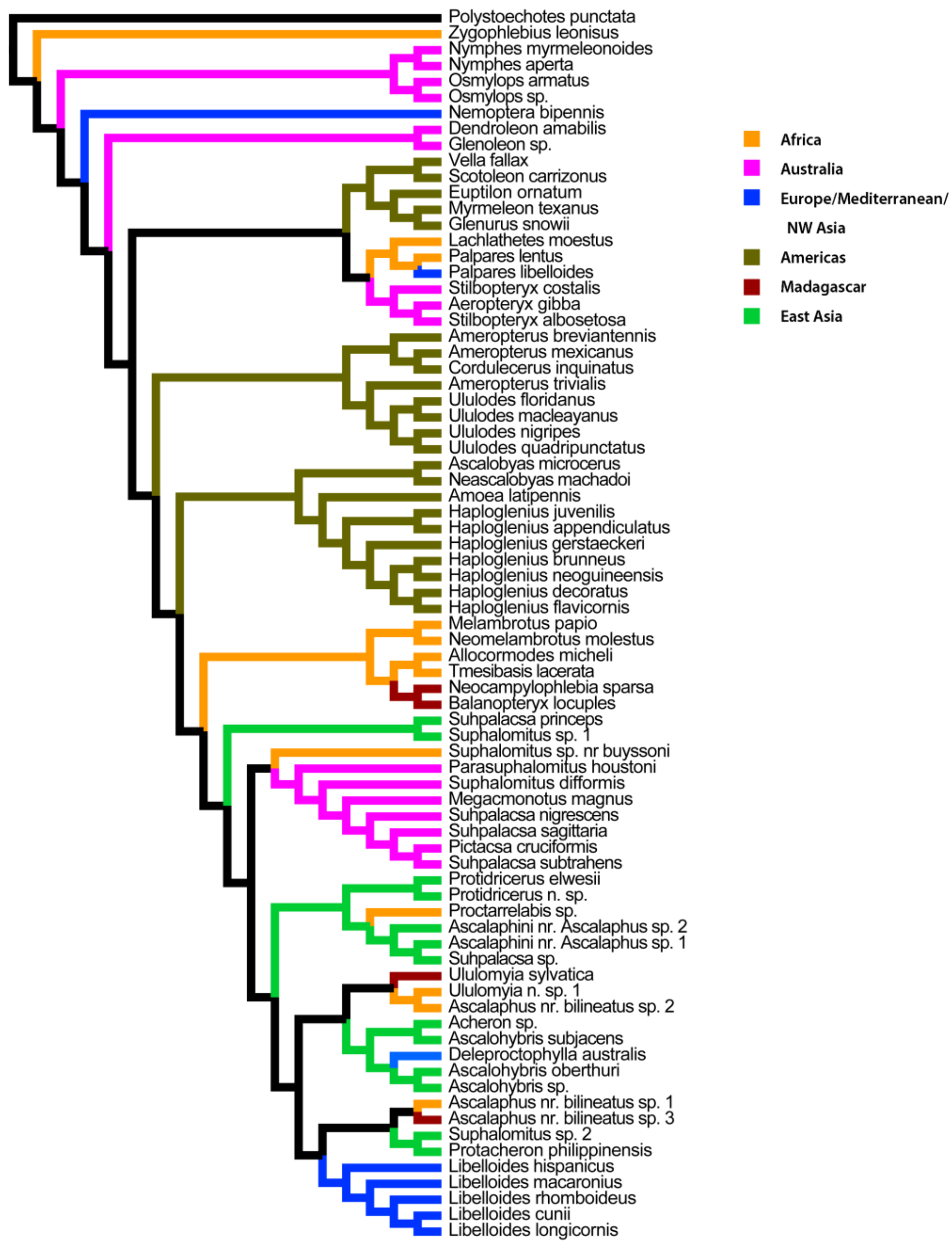


Fig. 11.—Parsimony cladogram color-coded to indicate geographic distributions of component taxa. Most suprageneric taxa of Ascalaphidae and Myrmeleontidae, as they currently are defined, appear to represent non-monophyletic units (see Figs. 9 and 10). Taxa with the closest phylogenetic relationships, however, appear to occur in common geographic regions, at least at the continental level.

Table 1. Major treatments of tribes of Ascalaphidae by various authors.

	v. d. Weele 1909	Navás 1912b	Navás 1912c	Navás 1919	Orfila 1949	Tjeder 1972	Penny 1982	New 1984	Tjeder 1992	current tribe
Haplogleniinae	none	Episperchini	Episperquinos				Haplogleniini			Haplogleniini
	none		Neuroptinginos		Verticillecerini		Verticillecerini			Verticillecerini
	none								Allocormodini	Allocormodini
	none								Campylophlebiini	Campylophlebiini
	none								Melambrotini	Melambrotini
	none								Proctolyrini	Proctolyrini
	none								Tmesibasini	Tmesibasini
Ascalaphinae	Acmonotini	Acmonotinos	Acmonotinos	Suhpalacsini[2]				Suhpalacsini[2]		Suhpalacsini
	Ascalaphini[1]		Ascalafinos			*-revised concept				none
	Encyoposini		Encioposinos							Encyoposini
	Hybrisini		Hibrisinos							Hybrisini
	Proctarrelabrini		Proctarrelabrinos							Proctarrelabrini
	Suhpalacsini[1]		Sufalacsinos	Suhpalacsini[2]				Suhpalacsini[1]	Ascalaphini[2]	Ascalaphini
	Ululodini	Ululodinos	Ululodinos							Ululodini
									Ululomyiini	Ululomyiini

Notes: Navás (1919) revised the definition of Suhpalacsini[1] and sunk Acmonotini within it (=Suhpalacsini[2]). Tjeder (1972) revised the type concept of genus *Ascalaphus* , moving most of the species out of the genus (and thus out of the tribe Ascalaphini[1]), whose males have the ectoprocts well-developed, to *Libelloides* Schäffer, but without addressing the issue of tribal placements. New (1984) was vague in his treatment of the Australian owlflies with regards to tribal placement but seemed to tentatively accept placement of all Australian taxa within Suhpalacsini[2] under Navás's (1919) concept. Tjeder (1992) reinterpreted Ascalaphini[2] to include only genera whose males have the ectoprocts undeveloped, which corresponds, in part, with van der Weele's original definition of Suhpalacsini[1] before its modification by Navás (1919). He did not address tribal placement for *Libelloides* species formerly placed in Ascalaphini, nor for related genera.

Table 2. Myrmeleontiformia exemplars included in this study for molecular sequencing and/or morphological scoring. Amplifications: 1=successful; 0=unsuccessful.

family	subfamily	tribe	exemplar	sex	JRJ#/GB	16S	18S	COI	Collection data or reference(s)
Polystoechotidae			*Polystoechotes punctata* (Fabricius, 1793)	?	10238	1	1	1	IDAHO: Butte Co.; Hwy 20 16 mi. E. Arco, Big Lost River Rest Area, el. 4987', 28-VII-08, A.R. Gillogly 43°32.913'N, 113°00.454'W
Psychopsidae	Zygophlebiinae		*Zygophlebius leoninus* Navás, 1910	male	10296	1	1	1	S. AFRICA: Mpumalanga, Snyman Estate, Marloth Park, 25.35412° S, 31.79897° E, 222 m, 2011-xii-16, J.Jones, L.Snyman, MV/tungsten light
Nymphidae			*Nymphes aperta* New, 1982	female	10258	1	1	1	AUSTRALIA: New South Wales North bank of Coloboalli Ck. 35°14.789'S, 147°19.191'E South of Wagga Wagga I-03-2011, 286m, MV light, K. Hill & D. Marshall
			Nymphes myrmeleonoides Leach, 1814	female	10257	1	1	1	AUSTRALIA: New South Wales Weddenburn, 75/203 Fairburn Rd S. of Sydney (Britton residence) I-1-2011, 135m, 34°09.009'S, 150°49.789'E K. Hill & D. Marshall, MV light
			Osmylops armatus (McLachlan, 1867)	male	10259	1	1	0	AUSTRALIA: New South Wales Weddenburn, 75/203 Fairburn Rd S. of Sydney (Britton residence) I-1-2011, 135m, 34°09.009'S, 150°49.789'E K. Hill & D. Marshall, MV light
			Osmylops sp.	?	10101	1	1	1	AUSTRALIA: SE Queensland Brisbane Forest Pk, Scrub Rd S 27.427, E 152.841 13.xii.2007-17.i.2008; Malaise over shallow creek in rainforest S. L. Winterton & J. S. Bartlett
Nemopteridae	Nemopterinae		*Nemoptera bipennis* (Illiger, 1812)	?	10131	1	1	1	PORTUGAL: Trais-os-Montes e Alto Douro Province, Vila Real District, Escalhão, fields above road, 40.98175°N, 6.93246°W, elev. 546 m, 2011-vi-19, J. R. Jones
Myrmeleontidae	Myrmeleontinae	Acanthaclisini	*Vella fallax* (Rambur, 1842)	male	10095	1	1	1	USA: TEXAS: Brewster Co., FM 2627, canyon W parking area #3, 79 air km SE Marathon, MV light, 29°32'47" N, 102°56'18" W, 776m, 2009-viii-19, J. R. Jones, M. A. Guaro
		Brachynemurini	*Scotoleon carrizonus* (Hagen, 1888)	?	10309	1	1	1	USA: AZ: Cochise Co.: 6.5 air km EESE jct I10 & AZ Hwy 186 in Willcox, 32.24125°N 109.76507°W +/-50m WGS84 8.viii.2010 JDOswald BRDiehl ex MV light

Table 2. Cont.

family	subfamily	tribe	exemplar	sex	JRJ#/GB	16S	18S	COI	Collection data or reference(s)
Myrmeleontidae	Myrmeleontinae	Dendroleontini	*Dendroleon amabilis* (Gerstaecker, 1885)	?	10310	1	1	1	AUSTRALIA: South Australia: Wilmington, Beautiful Valley Caravan Park, I-07-2011, 340m 32°39.703'S, 138°06.591'E K. Hill & D. Marshall,
			Glenoleon sp.	?	10311	1	1	1	AUSTRALIA: New South Wales: Condobolin Caravan Park, next to Lachlan River, I-12-2011, 201m. 33°05.600'S, 147°08.760'E K. Hill & D. Marshall, Park Lights
		Myrmeleontini	*Myrmeleon texanus* Banks, 1900	male	10254	1	1	1	USA: TEXAS: Leon Co., FM Rd 39, 8.5 km N Flynn, sand flats, MV light, 152 m, 31.22635°N, 96.12896°W, 2010-ix-29, J. R. Jones
		Nemoleontini	*Euptilon ornatum* (Drury, 1773)	?	10312	1	1	1	USA: FLORIDA: Highlands Co. Highland Park Estates, site 4 27.33398°N, 81.34355°W VII-14-2010, M. Deyrup, K. Dearborn, J. Dunlap, flight trap, Florida scrub
			Glenurus snowii Banks, 1907	male	10264	1	0	1	USA: ARIZONA: Pima Co., Brown Canyon mouth, 1158 m, 31.75978° N, 111.53322° W, 2012.vii.8 J. R. Jones, A. Davila-Flores, MV, sweep
	Palparinae	Palparini	*Lachlathetes moestus* (Hagen, 1853)	female	10304	1	1	1	RSA: Limpopo, Hoedspruit: Swadini, S 24°30.666, E 30°50.075 15 May 2011 Coll: L.P. Snyman
			Palpares lentus Navás, 1912	male	10299	1	1	0	RSA: Mpumulanga, Marloth 25°21'14.08"S 31°47'58.12"E Alt.219m (12V Black light trap) 28.XI.2011 Coll. L.P. Snyman
			Palpares libelluloides (Linnaeus, 1764)	male	10091	1	1	1	CROATIA: Istria County, 3 air km S Premantura, 13 m 44°46'28.19"N, 13°54'42.47"E, 2008-vi-30, J. R. Jones, sweeping
	Stilbopteryginae	Stilbopterygini	*Aeropteryx gibba* Riek, 1976	male	10239	1	1	1	Australia: N.T. ~30 km SW of Katherine at a rest stop on Victoria Hwy 30 Nov. 2011 K. Hill, D. Marshall MV light
			Stilbopteryx albosetosa Riek, 1976	female	10247	1	1	1	Australia: N.T. Keep River N.P. Gurrandaling [spelling?] Trail on sandstone outcrop 17 Nov 2011 K. Hill, D. Marshall MV light
			Stilbopteryx costalis Newman, 1838	female	10226	1	1	1	AUSTRALIA: New South Wales Wedderburn, 75/203 Fairburn Rd S. of Sydney (Britton residence) I-1-2011, 135m. 34°09.009'S, 150°49.789'E K. Hill & D. Marshall, MV light
Ascalaphidae	Haplogleniinae	Haplogleniini	*Amoea latipennis* (Navás, 1912)	male	10123	1	1	0	Guat Peten Nitum 11 VII 10 J. Monzon

Table 2. Cont.

family	subfamily	tribe	exemplar	sex	JRJ#/GB	16S	18S	COI	Collection data or reference(s)
Ascalaphidae	Haplogleniinae	Haplogleniini	*Ascalobyas microcerus* (Rambur, 1842)	female	10215	1	1	0	GUAT. El Progreso El Jicano lo de Chiva 340 m. 4 Junio 2011 Monzón
			Neascalobyas machadoi (Penny, 1982)	male	00255	1	0	1	BRASIL, AM, Itacoatiara Madeireira MIL, 0245106-583911W, 29-30.xi.2005
			Haploglenius appendiculatus (Fabricius, 1793)	male	10175	1	1	1	USA: Mississippi, Just outside Natchez S.P., 15 May 2011 K. Hill, D. Marshall, fluttering on ground at 12:00 pm
			Haploglenius brunneus m.s.	female	10128	1	1	0	GUATEMALA: Izabal Morales, Finca Firmeza del Banco, Sierra de Caral, 600m, 15.40715,-88.69626 2010-ix-7 Monzón [Firmeza X IX 10 JMS]
			Haploglenius decoratus m.s.	male	00632	1	0	1	BRASIL, AM, Pr. Figueiredo Rod. 240, km-24, Ramal São Francisco 29-31.x.2008
			Haploglenius flavicornis McLachlan, 1871	male	10209	1	1	0	Guatemala: Baja Verapaz Ranchitos del Quetzal. 26 VII 2011 J. MONZON
			Haploglenius gerstaeckeri (van der Weele, 1909)	female	01042	0	0	1	BRASIL, BA, Cachoeira Faz. Vila Rial, 143623S - 385347W, 200 m, 14.v.2007, J.A. Rafael & F.F.Xavier Fº., luz
			Haploglenius juvenilis (McLachlan, 1871)	male	10265	1	1	1	USA: ARIZONA: Pima Co., Brown Canyon mouth, 1158 m, 31.75978° N, 111.53322° W, 2012.vii.8 J. R. Jones, A. Davila-Flores, MV, sweep
			Haploglenius neoguineensis Navás, 1912	male	10182	1	1	1	Costa Rica: Guanacoste Province, Palo Verde National Park, field station, black light, 10.VI.2011 Kevin Henson
		Allocormodini	*Allocormodes micheli* m.s.	male	00021	0	0	1	21-V-03 BURKINA Bassora J. BOUYER
		Melambrotini	*Balanopteryx locuples* Karsch, 1889	female	00411	1	0	1	MADAGASCAR: Antsiranana Foret Ambato, 26.6 km 33° NE Ambanja elev 150 m 8 December 2004 13° 27' 52" S 048° 33' 06"E
			Melambrotus papio Tjeder, 1992	male	00675	1	1	1	South Africa: E. Cape 6 km N. Steytlerville; 520 m, malaise, 33°16.72'S 24°22.51'E, 16-23 Nov 1999, M.E. Irwin, E.J. Schlinger, F.D. Parker
			Neocampylophlebia sparsa van der Weele, 1909	male	00706	1	1	1	MADAGASCAR: Province Fianarantosa, Ranomafana National Park, ValBio Centre 21°15.260'S, 47°25.299'E 15-17.i.2007, at lights
			Neomelambrotus molestus Tjeder, 1992	?	GB	1	0	1	Sole et al. 2013

Table 2. Cont.

family	subfamily	tribe	exemplar	sex	JRJ#/GB	16S	18S	COI	Collection data or reference(s)
Ascalaphidae	Haplogleniinae	Tmesibasini	*Tmesibasis lacerata* (Hagen, 1853)	male	10306	1	1	1	RSA: Gauteng, Kwalata Nature Reserve (Dinokeng) -25.392837°E, 28.332396°S, alt: 1122m, 9.ii.2012 LP Snyman
		no placement	*Protidricerus elwesii* (McLachlan, 1891)	male	10253	1	1	0	TAIWAN: Kaohsiung Co. Shanping Forest Reserve Station, 9 km SE Liouguei, 700m 22°58'2"N, 120°41'14"E sweeping 23-VI-2004 J.R.Jones
			Protidricerus n. sp.	female	10189	1	1	1	PHILIPPINES: Palawan, Brgy. Ilihan Roxas, Sitio Tararaw, Tararaw Creek, 15-VI-2011 D. Mohagan
	Ascalaphinae	Ululodini	*Ameropterus breviantennis* Penny, 1982	male	10233	1	1	1	GUATEMALA, Huehuetenango. Barillas, San Ramon. Cerca de Rio Bravo 550 m. 18 MAYO 2012 15.884937 -91.230747 Col. Monzón, Composeco
			Ameropterus mexicanus (van der Weele, 1909)	male	10023	1	1	1	Fortuna, Vivero, to lights 31-VIII-08 A Gillogly & A. Smith Panama "32"
			Ameropterus trivialis (Gerstaecker, 1888)	male	10029	1	1	1	"Panama: Darien Prov. Cana Station 10-V-08 to lights Gillogly"
			Cordulecerus inquinatus Gerstaecker, 1888	male	10232	1	1	1	COSTA RICA, Alajuela Dept. Camino a Reserva Manuel Antonio Brenes, en el camino. 760 msnm. 26 ABRIL 2012 10.230509 -84.560110 Col. Monzón y Camposeco (back:) CR. Ramon 26 IV 2012
			Ululodes floridanus (Banks, 1906)	male	10041	1	1	0	USA: TEXAS: Brazos Co., College Station: Lick Creek Park, 30°33'48.4"N, 96°13'5"W, 66 m, 2009-vi-20, J.R.Jones, M.A.Guaro, MV light
			Ululodes macleayanus (Guilding, 1823)	male	10050	1	1	1	USA: TEXAS: Dimmit Co. Chaparral Wildlife Manage. Area Pasture #7, Headquarters, 175 m, 28°18'41.8"N,99°24'25.2"W, 2009-iv-25 J. R. Jones, MV light
			Ululodes nigripes Banks, 1943	female	10071	1	1	1	USA: TEXAS: Real Co., Pond Estate, 22.7 air km N, Barksdale, MV light, 585m, 29.91881° N, 99.96289° W, 2010-ix-5, J. R. Jones
			Ululodes quadripunctatus (Burmeister, 1839)	male	10080	1	1	1	USA: TEXAS: Brazos Co., College Station: Lick Creek Park, 30.562885°N, -96.215633°W, 66m, 2009-vi-2, J. R. Jones, M. A. Guaro, MV light

Table 2. Cont.

family	subfamily	tribe	exemplar	sex	JRJ#/GB	16S	18S	COI	Collection data or reference(s)
Ascalaphidae	Ascalaphinae	Suhpalacsini	*Megacmonotus magnus* (McLachlan, 1971)	male	10157	1	1	1	AUSTRALIA: WA: Walyunga National Park; Malaise Trap 31°44'02"S, 116°03'39"E; 19-29.xii.1999;J&A.Skevington,C.Lambkin,P.Bouchar
			Parasuphalomitus houstoni New, 1984	male	10242	1	1	1	Australia: W.A. Southern Kimberlies. Gieke Gorge National Park NE of Fitzroy Crossing 24 Nov 2011 K. Hill, D. Marshall MV light
			Pictacsa cruciformis New, 1984	male	10241	1	1	0	Australia: QLD Flinders River xing on Burke Development Rd ~60 km S of Normanton 07 Dec 2011 K. Hill, D. Marshall MV light
		Ascalaphini	*Ascalaphus* nr. *bilineatus* sp. 1	female	10295	1	1	1	S. AFRICA: KwaZulu-Natal, Umlalazi Nature Reserve, 28.96250° S, 31.75876° E, 13 m, 2011-xii-7, J.Jones, L.Snyman, MV/tungsten light
			Ascalaphus nr. *bilineatus* sp. 2	female	10180	1	1	1	SOUTH AFRICA: Northern Cape: Kalahari Desert, Tswalu Reserve, dune, 11.xii.2008; -27.283,
			Ascalaphus nr. *bilineatus* sp. 3	female	10229	1	1	1	MADAGASCAR: Atsinanana, 11 air km N Toamasina, adjacent to Ivoloina Parc Zoologique,
			Ascalaphini nr. *Ascalaphus* sp. 1	female	10289	1	1	0	VN.XX.BMR Vietnam, Bach Ma near rubber plantation 16 May 2012 Hill, Marshall
			Ascalaphini nr. *Ascalaphus* sp. 2	female	10286	1	1	1	VN.XX.CPV Vietnam Cuc Phuong N. P. 24 May 2012 Hill, Marshall, Du MV light
		Hybrisini	*Acheron* sp.	male	10280	1	1	1	VN.VC.MLI Vietnam Meh Linh Biological Station 31 May 2012 Hill, Marshall
			Ascalohybris oberthuri (Navás, 1923)	male	10177	1	0	1	THAILAND Chaiyaphum Pa Hin Ngam NP, Nature trail at Lan Hin Nau, 15°37.615'N, 101°23.436'E 668m, Malaise trap 1-_ix.2006 Katae Sa-nog & Buakaw Adnafai leg. 1845
			Ascalohybris subjacens (Walker, 1853)	?	GB	1	1	1	Cheng et al. 2014; Yun et al. 2012*
			Ascalohybris sp.	male	10270	1	1	0	VN.XX.BMV Vietnam Bach Ma nr base hotel/visitors area 18 May 2012 Hill, Marshall, Pham, etc MV light
			Protacheron philippinensis (van der Weele, 1904)	male	10035	1	0	1	PHILIPPINES, Bukidnon Province, Musuan Barangay, Mt. Musuan, 07° 52' 49" N, 125° 04' 03" E, 485 m, 2007-V-23–24 J. R. Jones, MV light sheet

Table 2. Cont.

family	subfamily	tribe	exemplar	sex	JRJ#/GB	16S	18S	COI	Collection data or reference(s)
Ascalaphidae	Ascalaphinae	no placement	*Deleproctophylla australis* (Fabricius, 1787)	male	10149	1	1	1	CROATIA: Istria County, 3 air km S Premantura, 13 m 44°46'28.19"N, 13°54'42.47"E, 2008-vi-30, J. R. Jones, sweeping
			Libelloides cunii (Navás, 1901)	male	10145	1	1	1	PORTUGAL: Trais-os-Montes e Alto Douro Province, Vila Real Council, Vila Real municipality, 41.27706°N, 7.87245°W, 870 m, 2011-vi-18, J. Oswald, B. Diehl
			Libelloides hispanicus (Rambur, 1842)	male	10148	1	1	1	PORTUGAL: Trais-os-Montes e Alto Douro Province, Vila Real Council, adjacent to Olo River, 41.37743°N, 7.81006°W, 970 m, 2011-vi-18, J.
			Libelloides longicornis (Linnaeus, 1764)	male	10129	1	1	1	PORTUGAL: Trais-os-Montes e Alto Douro Province, Vila Real Council, Vila Real, Lamas de Ola, Tojal, 41.37081°N, 7.80184°W, 990 m, 2011-vi-18, J. R. Jones
			Libelloides macaronius (Scopoli, 1763)	male	10150	1	1	1	SLOVENIA: Hrpelje-Kozina municipality: 1.3 air km SW Slope, 45°36'10.26"N,13°58'48.58"E, 546 m, 2008-vi-26 J. R. Jones, sweeping
			Libelloides rhomboideus (Schneider, 1845)	?	GB	1	1	0	Winterton et al. 2010
		Proctarrelabrini	*Proctarrelabis* sp.	male	10174	1	1	1	South Africa, Western Cape; 18 km S Sutherland; malaise in steep damp wash; 3-24.X.2004; ME
		Suhpalacsini	*Suhpalacsa nigrescens* New, 1984	male	10169	1	0	1	Mareeba, Qld. Feb. 2003 G. Monteith
			Suhpalacsa princeps Gerstaecker, 1894	male	10185	1	1	1	PHILIPPINES: Palawan, Brgy. Ilihan Roxas, Sitio Tararaw, Tararaw Creek, 15-VI-2011 D. Mohagan
			Suhpalacsa sagittaria New, 1984	male	10158	1	1	1	Australia: Queensland.Black Braes NP:Wolfram Springs. 13.7 km WSW of homestead. 980 m. Light Trap. 11.XI.2001. D.Yeates,C.Lambkin,N.Starick&J.Hamilton. GPS 19°34'58"S 144°04'57"E
			Suhpalacsa subtrahens (Walker, 1853)	male	10168	1	1	0	Australia: Queensland.Black Braes NP:Wolfram Springs. 13.7 km WSW of homestead. 980 m. In ravine,over waterholes. Malaise. 2-4.XI.2001. D.Yeates,C.Lambkin,N.Starick&J.Hamilton. GPS 19°34'58"S 144°04'57"E
			Suhpalacsa sp.	male	10272	1	1	1	VN.XX.TDT Vietnam Tam Dao 2 area at house 29 May 2012 Hill, Marshall, Long MV light

Table 2. Cont.

family	subfamily	tribe	exemplar	sex	JRJ#/GB	16S	18S	COI	Collection data or reference(s)
Ascalaphidae	Ascalaphinae	Suhpalacsini	*Suphalomitus difformis* (McLachlan, 1871)	female	10294	1	1	0	Australia: N.T. ~10 km E of Stuart Hwy on Barkly Stock Route. SE of Elliott 05 Dec 2011 K. Hill, D. Marshall MV light AU.NT.BSR 05 Dec 2011
			Suphalomitus sp. nr *buyssoni*	male	10179	1	1	1	SOUTH AFRICA: Northern Cape: Kalahari Desert, Tswalu Reserve, dune, 11.xii.2008; -27.283, 22.412; S.L. Winterton, M. Mansell, C. Sole
			Suphalomitus sp. 1	male	10271	1	1	1	VN.XX.TDT Vietnam Tam Dao 2 area at house 29 May 2012 Hill, Marshall, Long MV light
			Suphalomitus sp. 2	male	10285	1	1	0	VN.XX.CPV Vietnam Cuc Phuong N. P. 24 May 2012 Hill, Marshall, Du MV light
		Ululomyiini	*Ululomyia sylvatica* (Fraser, 1957)	male	10230	1	1	1	MADAGASCAR: Analanjirofo, 10.4 air km N Fenoarivo Atsinanana, Tampolo Forest Reserve, 17.28718° S, 49.40862° E, 18 m, 2012-i-3 J. R. Jones, S.Rahanitriniaina, MV light
			Ululomyia n. sp. 1	male	10176	1	1	0	Rep. South Africa: Limpopo Prov., Hans Merensky Nature Reserve, 23°42.95'S, 30°39.3'E, 434m elev. 10.I.05, lt. trap, coll. CS Chaboo

*not published; GB accession number KC413913

JRJ# refers to a project database maintained by the author. All specimens examined in this study have been provided a small archival database label either inserted in their vial or attached to their pin.

Table 3. Morphological data matrix for Myrmeleontiformia, as evaluated in this study.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Polystoechotes punctata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zygophlebius leonisus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Nymphes myrmeleonoides	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphes aperta	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmylops armatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmylops sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemoptera bipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Scotoleon carrizonus	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0
Dendroleon amabilis	1	0	0	1	0	1	0	1	0	0	0	0	0	?	0	1	0	0	0	0	0	?	0	1	0
Glenoleon osmyloides	1	0	0	1	0	1	0	1	0	0	0	0	0	?	0	1	0	0	0	0	?	0	0	1	0
Myrmeleon texanus	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0
Glenurus snowii	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	1	0
Euptilon ornatum	1	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	?	0	1	0
Vella fallax	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	?	0	1	0
Palpares libelloides	1	1	1	1	0	2	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	?	0	1	0
Palpares lentus	1	1	1	1	0	2	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	?	0	1	0
Lachlathetes moestus	1	1	1	1	0	2	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	?	0	1	0
Aeropteryx gibba	1	1	1	1	0	0	0	2	0	1	0	0	0	1	0	1	0	0	0	1	0	?	0	1	0
Stilbopteryx costalis	1	1	1	1	0	0	0	2	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0	1	0
Stilbopteryx albosetosa	1	1	1	1	0	0	0	2	0	1	0	0	0	1	0	1	1	0	0	1	?	0	0	1	0
Amoea latipennis	1	1	1	1	0	0	1	2	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Ascalobyas microcerus	1	1	1	1	0	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Neascalobyas machadoi	1	1	1	1	0	0	0	2	0	1	1	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Haploglenius brunneus	1	1	1	1	0	0	1	2	0	1	1	1	2	1	0	1	1	0	1	0	0	0	1	1	1
Haploglenius neoguineensis	1	1	1	1	0	0	1	2	0	1	1	1	2	1	0	1	1	0	1	0	0	0	1	1	1
Haploglenius decoratus	1	1	1	1	0	0	1	2	0	1	0	0	2	1	0	1	1	0	1	0	0	?	1	1	1
Haploglenius appendiculatus	1	1	1	1	0	0	1	2	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Haploglenius juvenilis	1	1	1	1	0	0	[0 1]	2	0	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Haploglenius flavicornis	1	1	1	1	0	0	1	2	0	1	0	0	2	1	0	1	1	0	1	0	0	0	1	1	1
Haploglenius gerstaeckeri	1	1	1	1	0	0	1	2	0	1	1	0	2	1	0	1	1	0	1	0	0	0	0	1	1
Allocormodes micheli	1	1	1	1	0	0	1	2	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Neocampylophlebia sparsa	1	1	1	1	0	0	1	2	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Balanopteryx locuples	1	1	1	1	0	0	1	2	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Tmesibasis lacerata	1	1	1	1	0	0	1	3	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Melambrotus papio	1	1	1	1	0	0	1	2	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Neomelambrotus molestus	1	1	1	1	0	0	1	2	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Protidricerus elwesii	1	1	1	1	1	0	1	2	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Protidricerus n. sp.	1	1	1	1	1	0	1	2	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Ameropterus breviantennis	1	1	1	1	1	0	1	2	1	1	0	0	0	0	0	1	1	0	1	1	0	?	0	1	1
Ameropterus mexicanus	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	1	0	?	0	1	1
Ameropterus trivialis	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1
Cordulecerus inquinatus	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1
Ululodes floridanus	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1
Ululodes macleayanus	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1
Ululodes nigripes	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1
Ululodes quadripunctatus	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	1	0	1	0	1	1
Megacmonotus magnus	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Parasuphalomitus houstoni	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	?	0	1	1
Pictacsa cruciformis	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Ascalaphus nr. bilineatus sp. 1	1	1	1	1	1	0	1	2	1	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Ascalaphus nr. bilineatus sp. 2	1	1	1	1	1	0	1	2	1	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Ascalaphus nr. bilineatus sp. 3	1	1	1	1	1	0	1	2	1	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Ascalaphini nr. Ascalaphus sp.	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Ascalaphini nr. Ascalaphus sp.	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Ululomyia sylvatica	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	?	0	1	1
Ululomyia n. sp. 1	1	1	1	1	1	0	1	2	1	1	0	0	1	1	0	1	1	0	1	0	0	?	0	1	1
Acheron sp.	1	1	1	1	1	0	1	2	1	1	0	0	2	1	0	1	1	0	1	0	0	0	0	1	1
Ascalohybris oberthuri	1	1	1	1	1	0	1	2	1	1	0	0	2	1	0	1	1	0	1	0	0	?	0	1	1
Ascalohybris subjacens	1	1	1	1	1	0	1	2	1	1	0	0	3	1	0	1	1	0	1	0	0	0	0	1	1
Ascalohybris sp.	1	1	1	1	1	0	1	2	1	1	0	0	2	1	0	1	1	0	1	0	0	?	0	1	1
Protacheron philippinensis	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Deleproctophylla australis	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	?	0	1	1

Table 3. Morphological data matrix for Myrmeleontiformia, cont.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Libelloides cunii	1	1	1	1	1	0	1	2	1	1	0	0	?	1	0	1	1	0	1	0	0	?	0	1	1
Libelloides hispanicus	1	1	1	1	1	0	1	2	1	1	0	0	4	1	0	1	1	0	1	0	0	0	0	1	1
Libelloides longicornis	1	1	1	1	1	0	1	2	1	1	0	0	4	1	0	1	1	0	1	0	0	0	0	1	1
Libelloides macaronius	1	1	1	1	1	0	1	2	1	1	0	0	4	1	0	1	1	0	1	0	0	0	0	1	1
Libelloides rhomboideus	?	?	?	1	?	?	1	2	?	1	0	0	?	1	0	1	1	0	1	0	0	?	0	1	1
Proctarrelabis sp.	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Suhpalacsa nigrescens	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Suhpalacsa princeps	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Suhpalacsa sagittaria	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Suhpalacsa subtrahens	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Suhpalacsa sp.	1	1	1	1	1	0	1	2	1	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Suphalomitus difformis	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1
Suphalomitus sp. nr. buyssoni	1	1	1	1	1	0	1	2	1	1	0	0	5	1	0	1	1	0	1	0	0	?	0	1	1
Suphalomitus sp. 1	1	1	1	1	1	0	1	2	1	1	0	0	5	1	0	1	1	0	1	0	0	?	0	1	1
Suphalomitus sp. 2	1	1	1	1	1	0	1	2	1	1	0	0	0	1	0	1	1	0	1	0	0	?	0	1	1

Table 4. Oligonucleotide primers used in this study.

locus and domain	domain	primer name	sequence	length	reference
Cytochrome oxidase 1 (COI)	2	C1-J-2195	5'- TTG ATT TTT TGG TCA CCC TGA AGT -3'	24	Winterton et al. 2010
	2	TL2-N-3014	5'- TCC ATT GCA CTA ATC TGC CAT ATT A -3'	25	Winterton et al. 2010
16S rRNA	1	LR-J-12887	5'- CCG GTT TGA ACT CAG ATC ATG T -3'	22	Winterton et al. 2010
	1	SR-N-13398	5'- CRC YTG TTT AWC AAA AAC AT -3'	20	Winterton et al. 2010
18S rRNA	1	20F	5'- CTG GTT GAT CCT GCC AG -3'	17	Winterton et al. 2010
	1	519R	5'- GWA TTA CCG CGG CKG CTG -3'	18	Winterton et al. 2010
	2	Sia	5'- CCT GAG AAA CGG CTA CCA CAT C -3'	22	Winterton et al. 2010
	2	Sbi	5'- GAG TCT CGT TCG TTA TCG GA -3'	20	Winterton et al. 2010
	3	18H	5'- GCT GAA ACT TAA AGG AAT TGA CGG AAG GGC AC -3'	32	Winterton et al. 2010
	3	18L	5'- CAC CTA CGG AAA CCT TGT TAC GAC TT -3'	26	Winterton et al. 2010

Table 5. PCR thermocycling regimes followed in this study.

cycling profile	hot start	denature	anneal	extension	goto	denature	anneal	extension	goto	denature	anneal	extension	goto	final ext.	cool	cycles
COI (Emerald[1])	94° (2:00)	94° (0:40)	52° (0:50)	72° (1:00)	—	—	—	—	—	—	—	—	—	72° (10:00)	4° (∞)	35
COI (5' HotMM[2])	94° (2:00)	94° (0:40)	52° (0:50)	65° (1:00)	—	—	—	—	—	—	—	—	—	65° (10:00)	4° (∞)	35
COI TD1 (5' HotMM[2])	95° (2:00)	94° (0:40)	49° (0:50)	65° (1:00)	6x	94° (0:40)	51° (0:50)	65° (1:00)	6x	94° (1:00)	53° (0:50)	65° (1:00)	28x	65° (10:00)	4° (∞)	TD[3]
16S (Emerald[1])	95° (3:00)	92° (0:15)	48° (0:45)	72° (2:30)	6x	92° (0:15)	52° (0:45)	72° (2:30)	30x	—	—	—	—	72° (7:00)	4° (∞)	TD[3]
16S TD1 (5' HotMM[2])	95° (3:00)	92° (0:15)	48° (0:45)	65° (2:30)	6x	92° (0:15)	52° (0:45)	65° (2:30)	30x	—	—	—	—	65° (7:00)	4° (∞)	TD[3]
16S TD2 (5' HotMM[2])	95° (3:00)	92° (0:15)	44° (0:45)	65° (2:00)	6x	92° (0:15)	48° (0:45)	65° (2:00)	6x	92° (0:15)	52° (0:45)	65° (2:00)	28x	65° (7:00)	4° (∞)	TD[3]
18S (Emerald[1])	95° (3:00)	95° (1:00)	50° (1:00)	72° (2:00)	—	—	—	—	—	—	—	—	—	72° (7:00)	4° (∞)	30
18S (5' HotMM[2])[4]	95° (3:00)	95° (1:00)	55° (1:00)	65° (2:00)	—	—	—	—	—	—	—	—	—	65° (7:00)	4° (∞)	30
18S TD1 (5' HotMM[2])	95° (3:00)	94° (1:00)	51° (0:45)	65° (1:30)	7x	94° (1:00)	54° (0:45)	65° (1:30)	7x	94° (1:00)	57° (0:45)	65° (1:30)	21x	65° (10:00)	4° (∞)	TD[3]

[1] Emerald = EmeraldAmp MAX PCR Master Mix; [2] 5' HotMM = 5 PRIME HotMasterMix; [3] TD = touchdown protocol; [4] used for 18S domains 2 and 3

Table 6. Partitioning schemes used in RAxML analysis of combined molecular data.

partition	syntax	explanation
i	N/A	Unpartitioned.
ii	DNA, 16S=1-527 DNA, 18S=528-1179 DNA, COI=1180-2045	Each gene treated as a separate partition.
iii	DNA, 16S=1-527 DNA, 18S=528-1179 DNA, COI_1=1181-2045\3 DNA, COI_2=1182-2045\3 DNA, COI_3=1180-2045\3	16S and 18S treated as independent partitions, but COI separated into individual partitions for first, second and third base pair positions.
iv	DNA, 16S=1-527 DNA, 18S=528-1179 DNA, COI_1=1181-2045\3 DNA, COI_23=1182-2045\3,1180-2045\3	16 and 18S, and COI first codon positions separated into individual partitions, and COI second and third base pair positions combined into a single partition. This approach agrees with the outputs from PartitionFinder, which suggested using GTR+G for position 1 but GTR+I+G for position 2 and TVM+I+G for position 3. In RAxML, TVM+I+G is executed in the same way as GTR+I+G, agreeing with the model suggested for base position 2.